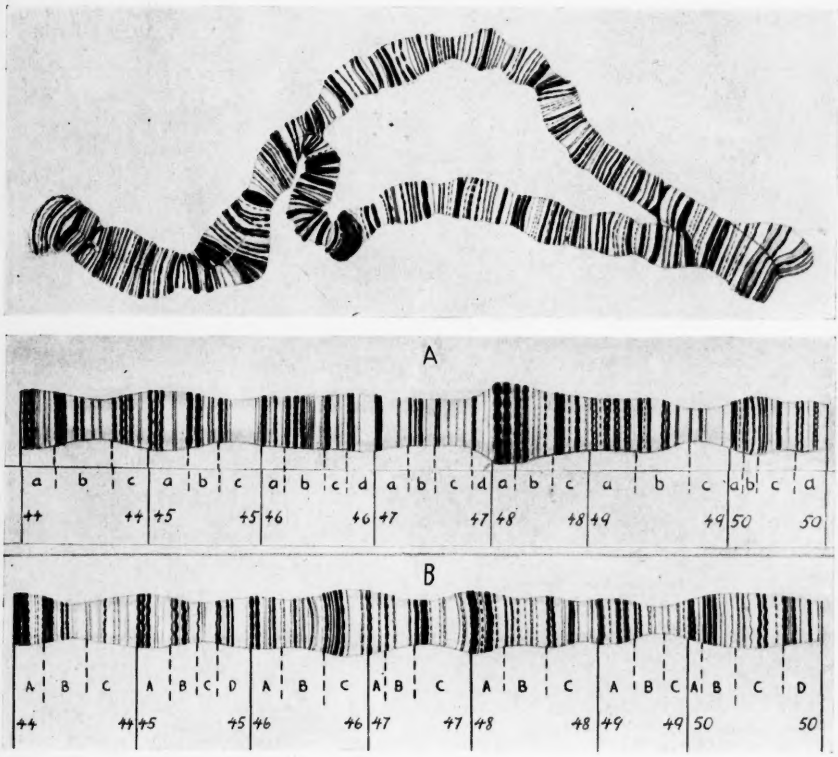
The Journal of HEREDITY



CHROMOSOME PATTERN
(SEE PAGE 265)

A Visit with Mendel

Sex-Inversion in the Peafowl

Dog Crosses and Human Crosses

A Chromosome-Doubled Lactuca Hybrid

VOLUME 33 JULY, 1942 NUMBER 7

The American Genetic Association

An incorporated organization devoted to promoting a knowledge of the laws of heredity and their application to the improvement of plants, animals, and human racial stocks

DAVID FAIRCHILD, President Vice-President, SEWALL WRIGHT Secretary, C. E. LEIGHTY
Treasurer, J. H. KEMPTON
Legal Advisor, STANTON C. PEELLE

EDITORIAL BOARD

Managing Editor, ROBERT C. COOK

M. DEMEREC GEORGE M. DARROW
H. J. MULLER R. R. GRAVES PAUL POPENOE

Members of the Council are ex-officio members of the Executive Board

COUNCIL

W. E. CASTLE, Emeritus Professor of Genetics, Harvard University, and Research Associate of the Carnegie Institution of Washington.
LEON J. COLE, Professor of Genetics, University of Wisconsin.
O. F. COOK, Bionomist in Charge of Breeding Investigations, U. S. Department of Agriculture.
DAVID FAIRCHILD, Agricultural Explorer, U. S. Department of Agriculture.
HARRY V. HARLAN, Senior Agronomist in Charge of Barley Investigation, U. S. Department of Agriculture.
SAMUEL J. HOLMES, Professor of Zoology, University of California, Berkeley, California.
MORLEY A. JULL, Department of Poultry Husbandry, University of Maryland, College Park, Md.
J. H. KEMPTON, Bureau of Plant Industry, U. S. Department of Agriculture.
W. V. LAMBERT, Associate-Director, Purdue University Agricultural Experiment Station, Lafayette, Indiana.
C. E. LEIGHTY, Agronomist in Charge of Dry Land Agriculture, U. S. Department of Agriculture.
MARCUS M. RHOADS, Department of Botany, Columbia University, New York City.
SEWALL WRIGHT, Professor of Zoology, University of Chicago.

ADVISORY COMMITTEE

W. S. ANDERSON, Genetics Department, University of Kentucky, Lexington, Kentucky.
E. B. BABCOCK, Genetics Department, University of California, Berkeley, California.
E. A. BESSEY, Professor of Botany, Michigan State College, Lansing, Michigan.
A. F. BLAKESLEE, Plant Geneticist, Carnegie Institution, Cold Spring Harbor, New York.
W. E. BRYAN, Professor of Plant Breeding, University of Arizona, Tucson, Arizona.
C. B. DAVENPORT, Carnegie Institution of Washington, Cold Spring Harbor, L. I., New York.
RUSSELL W. DUCK, Livestock Editor, *The Rural New Yorker*, Syracuse, N. Y.
R. A. EMERSON, Professor of Plant Breeding, Cornell University, Ithaca, New York.
C. P. GILLETTE, President, The Genetic Foundation, Fort Collins, Colorado.
C. M. GOETHE, Sacramento, California.
HARRISON R. HUNT, Professor of Zoology, Michigan State College, East Lansing.
H. S. JENNINGS, Professor of Zoology, Johns Hopkins University, Baltimore, Maryland.
D. F. JONES, Plant Breeder, Connecticut Agricultural Experiment Station, New Haven, Conn.
M. A. JULL, Senior Poultry Husbandman, U. S. Department of Agriculture, Washington, D. C.
F. B. LINFIELD, Director, Montana Experiment Station, Bozeman, Montana.
C. C. LITTLE, Director, Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine.
JAY L. LUSH, Professor in Animal Husbandry, Iowa State College, Ames, Iowa.
H. H. NEWMAN, Professor of Zoology, University of Chicago, Chicago, Ill.
T. S. PALMER, Expert in Game Conservation, U. S Dept. of Agriculture, Washington, D. C.
JOHN H. PARKER, Professor of Agronomy, Kansas State College, Manhattan, Kansas.
JOHN W. SCOTT, Professor of Zoology, University of Wyoming, Laramie, Wyoming.
A. D. SHAMEL, Physiologist, U. S. Department of Agriculture, Riverside, California.
GEORGE H. SHULL, Professor of Biology, Princeton University, Princeton, New Jersey.
EDMUND W. SINNOTT, Professor of Botany, Barnard College, Columbia University, New York City. (Representative of A. G. A. on Council of Amer. Assoc. for the Advancement of Science.)
W. W. SMITH, Professor of Animal Husbandry, Purdue University, Lafayette, Indiana.
A. B. STOUT, Director of Laboratories, New York Botanical Gardens, New York City.
W. T. SWINGLE, Plant Physiologist in Charge of Breeding Investigations, U. S. Department of Agriculture, Washington, D. C.
W. H. TOMHAVE, American Aberdeen-Angus Breeders' Association, Chicago, Ill.
H. E. WALTER, Professor of Biology, Brown University, Providence, Rhode Island.
H. J. WEBBER, Prof. Subtropical Hort., Citrus Experiment Station, Riverside, California.
E. N. WENTWORTH, Armours' Bureau of Agr'l Research and Economics, Chicago, Illinois.
P. W. WHITING, Zoological Laboratory, University of Pennsylvania, Philadelphia, Pa.

The JOURNAL OF HEREDITY is published monthly by the AMERICAN GENETIC ASSOCIATION at 32nd Street and Elm Avenue, Baltimore, Md., and 1108 Sixteenth St., N. W., Washington, D. C. Address all communications regarding editorial matters to Room 205, 1108 Sixteenth St., N. W., Washington, D. C. Communications regarding the business management of The JOURNAL OF HEREDITY may be addressed to the publication office, 32nd Street and Elm Avenue, Baltimore, Md., or to 1108 Sixteenth Street, N. W., Washington, D. C. Entered as second-class matter February 24, 1923, at the postoffice at Baltimore, Maryland. Acceptance for mailing at the special rate of postage provided for in section 1103, Act of October 3, 1917, authorized December 20, 1918.

Contents copyrighted 1942 by the American Genetic Association. Unauthorized reproduction of material from THE JOURNAL not permitted. The title "Journal of Heredity" is registered as a trade-mark in the U. S. Patent Office.

$3.50 a Year. 35c a Copy. Prices of back numbers on application.

The

Journal of Heredity

Vol. XXXIII **JULY, 1942** **No. 7**

CONTENTS

I Talked With Mendel
By C. W. Eichling, Sr. 243

Sex Inversion in the Peafowl
By T. H. Morgan 247

An Amphidiploid Lactuca
By Ross C. Thompson 253

The Pattern of Salivary Gland Chromosomes
By Elizabeth Goldschmidt 265

Notes and Reviews

Dog Crosses and Human Crosses (Rev. Stockard, *The Genetic and Endocrinic Basis for Differences in Form and Behavior.*)
By W. E. Castle 249

Plant Breeding—The Modern Way (Rev. of Hayes and Immer, *Methods of Plant Breeding*)
By O. E. White 264

Meeting of Scientific Photographers 264

Manx Genetic Justice 272

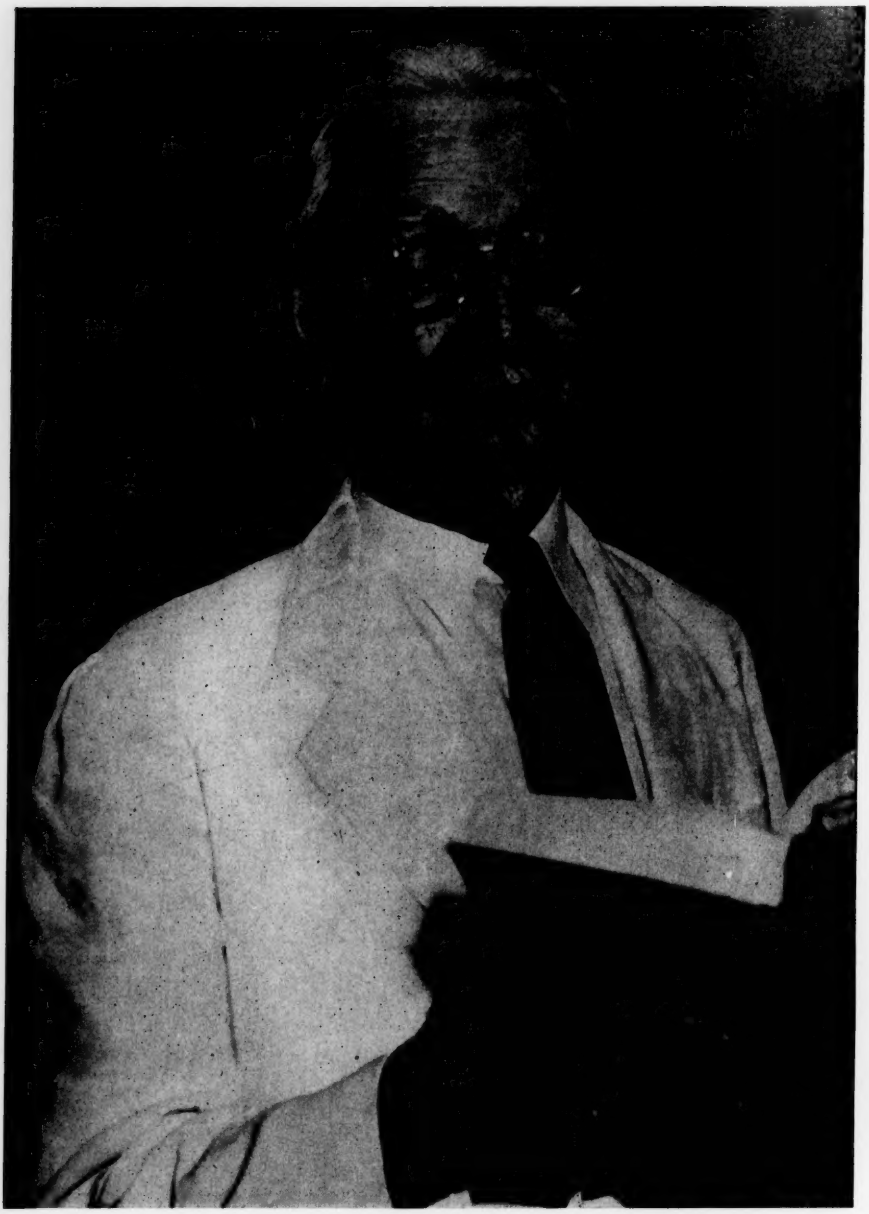
STUDENT SUBSCRIPTIONS

The **Journal** has obvious advantages as a supplementary text in genetics classes. Since genetics deals mainly with form and pattern differences in organisms the **Journal** offers an unexcelled introduction to current developments, which have an added interest and appeal on account of the large number of illustrations published.

Some years ago we tried the experiment of offering the **Journal** at a special student group subscription rate for classroom use. The plan was tried the first year by several of our members, and some of them are still using it every year, a convincing testimony to its value as a supplementary text.

STUDENT SUBSCRIPTIONS covering the academic year of nine months in groups of ten or more, may be ordered by members at one dollar ($1.00) each; four months for 50 cents. These special rates to students will be accepted only when applied for by members of the Association, in whose classes the **Journals** are to be used. The student subscriptions will be sent in bulk to the member in whose name they are ordered. Orders should be sent to the Washington office of the Association.

$3.50 a Year **35c the Copy**



C W. EICHLING, SR.

In the summer of 1878 Mr. Eichling, then a youngster of 22, spent an afternoon with Gregor Mendel in his garden.

I TALKED WITH MENDEL

C. W. EICHLING, SR.
New Orleans, Louisiana

EDITOR'S NOTE: *In the summer of 1878 a youthful representative of one of the large French plant specialty establishments called on the famous Abbott of Brünn. That same stripling now looks back over sixty-four years to give us a glimpse of the first geneticist. Mendel was born on July 22, 1822, so that this note approximately marks his 120th birthday.*

Mr. C. W. Eichling came by his interest in plants by both cultural and genetic inheritance, for he grew up in his father's greenhouses at Kaiserslautern, Germany. After working for a number of European horticultural establishments, Mr. Eichling came to the United States in 1882. Shortly after he opened a flower and seed store in New Orleans. He has lived and worked there ever since.

It is unfortunate that Mr. Eichling knew so little about Mendel's work when he visited the founder of genetics. Mendel's obvious reticence regarding his experiments is easily understood when we recall how completely they were ignored by the scientific world. Though this interview throws little light on the history of genetics, Mr. Eichling gives a charming account of a unique summer afternoon of two-thirds of a century ago.

IN the Summer of 1878 I was traveling representative for Louis Roempler, one of the large novelty plant-and-seed firms of Nancy, France. The exclusive nature of the plants and seeds, novelties and rare specimens I had to offer, limited by clientele to the larger horticultural establishments of Europe, including royal gardens, botanical gardens and large private estates.

I was on a trip which was to take nine months, and had been north as far as Denmark and east to the Russian border. I was to go south from there via Berlin and Leipzig to Erfurt, which was at that time the center of production of the highest class of vegetable and flower seeds as well as of rare and standard hothouse plants. At Herrenhausen, near Hanover, I called on Director Herman Wendland, superintendent of the royal botanical gardens. Even in those days Wendland was acknowledged the highest authority on palms. The royal parks and hothouses under his charge contained one of the most complete collections of palms to be found anywhere in Europe.

Not one of the leaders in the horticultural industry interviewed that Summer mentioned the name of Mendel. Not until I reached Erfurt and called on Ernest Benary, the Nestor of European seed growers and breeders, did I hear Mendel's name mentioned. It was in connection with mysterious results he was reported to have obtained in experiments with garden peas. This, of course, meant very little to me at that time, but history records that I was not alone in my ignorance regarding Mendel. Even the scientists of that period, including the great Swiss botanist Nägeli, had completely failed to grasp the significance of the Abbot's great contribution.

Benary personally conducted me through his extensive cultures of flower seeds for which hundreds of acres were under cultivation and at the time of my visit in full bloom. This was long before California had taken such an important place in the seed-growing game. Some of Benary's specialties were double Stock (*Matthiola*), double Petunia and *Primula sinensis*. While we were examining an open shed filled with potted Stocks he called my attention to several young men engaged in pollinating Petu-

nias for the production of doubles, the highest percentage attained at that time being about thirty. It was then that Benary mentioned Mendel at Brűnn and his experiments with garden peas, *Pisum sativum*. I told Benary that Brűnn was on my itinerary on my way from Prague to Vienna and he suggested that I try to meet the Abbot if possible. I did not get very specific information about Mendel's work from Benary, but I had met with such a cordial reception from that renowned seed grower that I felt in duty bound to carry out his request.

Let me state here that the traveling representative of a business house in Europe enjoys a much more respected position than the "drummer" in the United States. He is received with the same friendly respect as the head of the firm. This custom impressed me very favorably, as at that time I was only 22 years old and had scarcely been in Roempler's establishment in Nancy long enough thoroughly to familiarize myself with the large collection of novelties and standard commercial plants offered in our catalog.

Prophet Without Honor

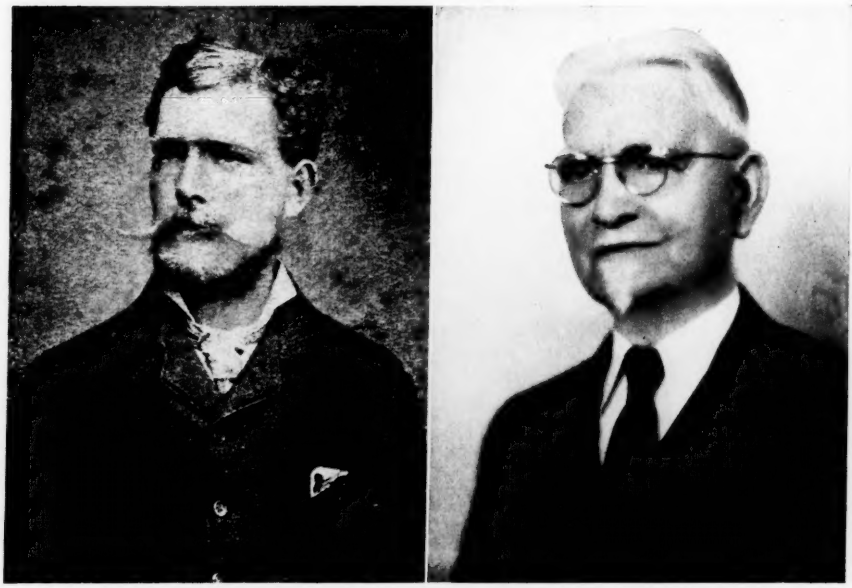
On my arrival at Brűnn I called on the only customer I had in the quaint old city of about 70,000 inhabitants. After our business was concluded, I asked about the Abbot Mendel. My customer stared at me in some astonishment and registered mild amusement at my inquiry. I was told that, while *der Herr Abt* was one of the best beloved clerics in Brűnn, not a soul believed his experiments were anything more than a pastime, and his theories anything more than the maunderings of a charming putterer.

The following morning I rang the door bell at the Augustinian Koenigin Kloster (Queen's Cloister) where Mendel was the Abbot with the title of Prelate. A monk spoke to me through a small lattice in a heavy wooden door, and took my card. In a few minutes I was admitted into a large hall from which a broad stairway led to the Abbot's reception room on the right.

My first impression was a genuine and pleasant surprise. My customer's account had built in my mind a picture of an old, wrinkled, spooky, monk. Coming toward me was a fine looking, spectacled priest, smiling and extending a welcoming hand. His countenance expressed both determination and kindliness. I judged him to be about fifty years old. He offered me a seat and having been told that German was the Abbot's favorite language we were soon in a lively conversation.

I told Mendel that Ernest Benary had requested me to call on him and I discovered then that Mendel knew of nearly all the important men in the plant and seed line. He asked about Victor Lemoine, the well known hybridizer of Nancy. I was able to tell him that, while my firm was Lemoine's strongest competitor in plant novelties, I personally was very friendly with the Lemoines and was often at their greenhouses and propagating benches where hundreds of large glass bells were used in those days for covering freshly made cuttings or grafts of rare varieties of *Aralias, Clematis*, etc. Long before Lemoine's novelties of *Gladiolus, Spirea* and hybrid *Syringas* were placed on the market, he had given to the world the first double Geranium, around 1865. It was a light pink and he named it for his wife, *Madame Lemoine*. The second double he introduced was a deep crimson named for his daughter, *Lucie Lemoine*.

We then perused my catalogue together, and Mendel displayed great interest in the rare plants I had to offer and asked many questions about their propagation. He was delighted with pictures taken in the wilds of Madagascar of several Cycadeae such as *Encephalartos* and *Cycas circinalis*, also tree ferns and tall *Chrysalidocarpus lutescens* palms. Our collector, a botanist named Humblot, a pupil of Godron, had sent home large cases full of seeds of the latter for my trade. I sold them under the old name of *Areca lutescens*. There was also a curious aquatic, *Ouvirandra fene-*



THEN AND NOW

Figure 2

On the left is a photograph of the author made in the summer of 1878, when he visited Gregor Mendel. On the right is a photograph made within the past year. As representative of a seed house specializing in hot house plants Mr. Eichling visited most of the great conservatories of Europe. Since he was only twenty-two years old his employer thought that the dignity of his position demanded a moustache and beard.

stralis, the skeleton leaves of which floated on running water kept at 80 degrees Fahrenheit.

The Garden

It was now mid-day and the monastery bell called to dinner to which the Abbot invited me. A substantial meal, served in the Abbot's study, consisted of soup, home grown vegetables, home made bread, exquisite ham and beer. After a little chat, the Abbot invited me to walk with him through his extensive gardens. The grounds were kept as clean as a pin. I was shown beds of well grown vegetables and fruit trees of many varieties, each tree with a label. Mendel pointed with pride to a pair of espaliers against a wall, well loaded with fruit. One of them was the old French pear *La Duchesse d'Angoulème,* which I happened to know from my father's collection of espalier fruit trees, on which I had had to study the art of pruning for correct branching and fruiting.

I repeat here that at the time I met Mendel I knew practically nothing of his discoveries and experiments and he forbore to enlighten me on the subject. He did show me several beds of green peas in full bearing, which he said he had reshaped in height as well as in type of fruit to serve his establishment to better advantage. I asked him how he did it and he replied: "It is just a little trick, but there is a long story connected with it which would take too long to tell." Mendel had imported over 25 varieties of peas, which shelled out readily, but did not yield very well because some of them were bush types. As I recall it, he said that he crossed these with his tall local sugar-pod types and now had tall shelling types, which were used at the monastery.

I told Mendel that I had promised to

make a report to Benary regarding these experiments, but Mendel changed the subject and asked me to inspect his hothouse. He was very proud of several well-grown ferns and two large *Philodendron pertusum*. A clump of *Aspidistra lurida* in one corner of a bench attracted my attention on account of its pronounced variegation. I asked Mendel how he managed to keep the stripes in such fine condition. He told me that he had lost several well-colored plants through reversion to the green because he over-fertilized them, and that since he starved his *Aspidistras* he had no trouble in keeping the variegation intact. Variegated *Aspidistras* were scarce in those days and before I left France my employer had requested me to watch out for well variegated plants and to buy all I could find. This information from Mendel became of great value to us.

Mendel asked me about my school days. I told him that besides several years of Latin and three years of French I went to New York in 1872 to study English. He was of the opinion that I should have gone through Heidelberg University. He became enthusiastic when he spoke of his own student years in Vienna and we even recalled some of our favorite student songs such as "Gaudeamus igitur" — "Vom Hoh'n Olymp" — "Edite, bibite collegiales," etc.

When I told him that I should be in Vienna the following day he visibly envied me this privilege and named several places of horticultural interest I should visit. Among these were the Imperial Gardens at Schönbrunn with their interesting greenhouses and collections of palms, of which I was especially fond. He also mentioned the famous, well trimmed hedge walls of immense height and beauty.

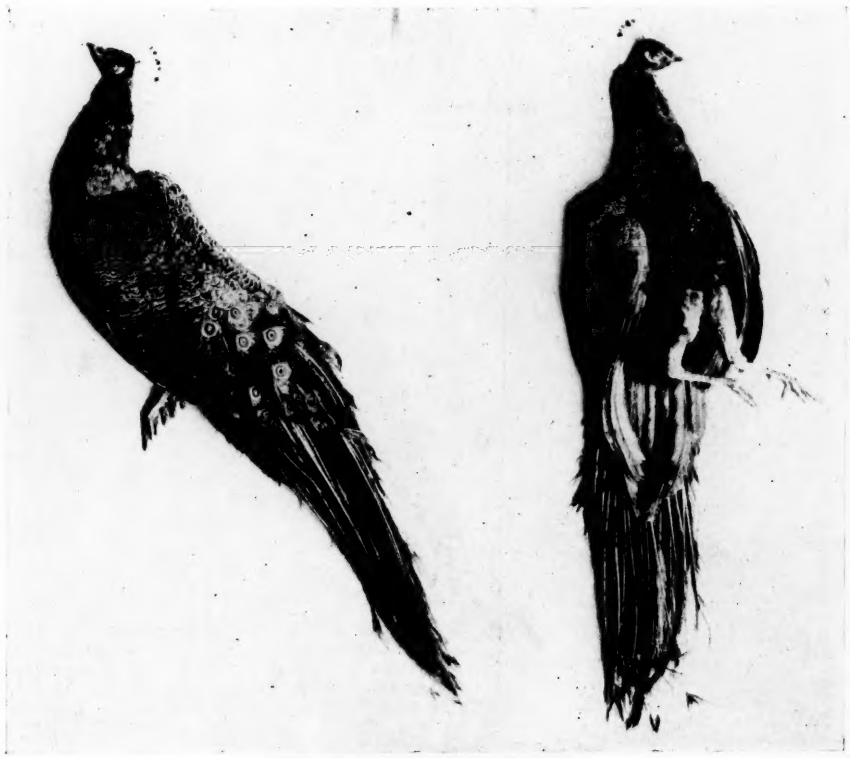
We now approached the extensive apiaries in which Mendel took great interest, especially since he had abandoned his research work with hybridization. Mendel understood his bees and they knew him and never stung him after they discovered that he was their friend. He imported queens from Italy and other countries, raised colonies and distributed them among his friends. Mendel's love for bees, fruit trees, vegetables and flowers and his successful studies of meteorology gave ample proof of his practical sense, which he used principally in the management of the monastery with its many branches such as dairies, vineyards, real estate, and gardens.

My time to leave had arrived, and I thanked the Abbot for his great kindness to me, a young stranger. I knew from his hearty handshake and his blessing that I had made a friend. He accompanied me to the gate and made me promise to call on him again. This was not to be, because other plans prevented my returning.

It is strange that when I asked Mendel about his work with peas, he deliberately changed the subject. It could not have been that he had any desire to withhold the facts from me, for he had published the two immortal papers on his discoveries a dozen years before. It would seem that a direct invitation to talk about what must have been a very important episode in his life would have eagerly been seized upon. Could it be that this reticence was due to the complete oblivion his publications had achieved? Actually to have found the key to the riddle of heredity, and to have his discovery completely ignored both by his friends and by the scientific public must have been a tragic blow. It has been said that Mendel's experiments with small animals were frowned on by his superiors, and possibly there was an inner conflict between his religious beliefs and his scientific interests. But the patronizing letter from Nagaeli, advising him to spend his time more profitably, would have been enough to quench the enthusiasm of a very hardy soul indeed. Be that as it may, by failing to draw the master out with a sympathetic question I missed a priceless chance, in that garden sixty-four summers ago, to hear from the lips of the founder of Genetics how he made the discovery which today is recognized as marking an epoch in the study of life.

SEX INVERSION IN THE PEAFOWL

T. H. Morgan
California Institute of Technology, Pasadena, California



THE SEX-INVERTED PEAHEN

Figure 3

Two views of the peahen taken in 1938 just after it had died. Notice the prominent "eyes" in the plumage in the view at the left.

SOME time in 1935 I heard that there was a peahen near Los Angeles that was changing its plumage to that of the male. I wrote to Mr. J. P. Scott asking him to let me have the bird after it died. This happened in 1938 and I got word from Mr. Scott that he would send the bird to me as soon as the heavy rains let up. In a day or two the bird was delivered. A letter from Mr. Scott enclosed a picture of the bird taken in 1935 and printed in the *Los Angeles Herald and Express* on April 6th. As shown in Figure 4 the peahen was, in 1935, in an intermediate stage. The legend below the picture reads:

Dropping her drab, female characteristics, Girlie, 13-year-old peahen, owned by J. P. Scott and Nellie Scott Traugott of Los Angeles, today appeared to be changing her sex. Top arrow points to her head feathers, which are becoming blue like a male's; second arrow to blue-centered green feathers, which she recently has grown and which only the male birds usually possess.

INITIAL STAGES

Figure 4

Newspaper photographs from Los Angeles *Herald* and *Express* of April 6, 1935.

A photograph of the dead bird in 1938 is shown in Figure 3. At that time Mr. Scott wrote me as follows:

In regards to the Peahen, it was about 16 years old, and was a present to us when about two years old, was just the ordinary plain peahen, laid eggs, and hatched her young until about 3 years before change in plumage, never had but the one pair of birds and I never saw it spread its tail as a male would, the male for a while after the change would spread before her, but did not seem to make any attempt to mate, the past year he has seemed to consider her just another male.

Inclosed find a picture and if you will notice the female tail feathers and the new male ones coming out.

In answer to a letter of mine, Mr. Scott made the following emphatic statement, viz., that it is quite certain that the peahen had laid eggs as there was no other female on the place.

The bird was skinned and the skin preserved. The carcass was opened and the abdominal organs examined. They were not in very good condition. A large lump was found near the posterior end surrounding a loop of the intestine but not attached to the intestine. It was three or four inches in diameter. I sent it to a pathologist who reported he found no cellular structure and it did not resemble in any way a cancer. Unfortunately the lump is lost. I found no trace of ovary or testes, but the organs of the abdominal cavity had begun to decay. No conspicuous gonads were found.

I have not had an opportunity to look through the literature except superficially. Reference to a similar change in a peahen in the Transactions of the Kentucky Academy of Sciences, Vol. IV, 1930, reads (in part) as follows:

The creature described was hatched in 1915 on the premises of Mr. S. D. May, of Salyersville, Kentucky. For a number of years after reaching maturity the fowl behaved in the usual manner, laying her quota of eggs each season, hatching her brood, and caring for them according to the orthodox method of her kind. In 1922, after moulting, the first evidence of a change appeared, in that she assumed partial male plumage. In two years the drab, subdued, brown plumage of the female was completely replaced by the gorgeous "blue of the beak; green and black of the back and wings; brown, green, violet and gold of the tail." The bird itself seemed to sense the fact of its beauty, and strutted about in the male fashion. The gorgeous typical male train was developed. The bird seemed to take great delight in rattling the shafts of the tail feathers so as to produce the characteristic masculine vibration. The voice equipment reacted male-like. In a word the fowl assumed the complete appearance of the male, and acted his part. In 1927 the bird died. No autopsy was performed and, of course, no histological examination of the gonad. It could not be ascertained whether or not this transformed individual ever became a functional male.

Changes similar to these have often been described for the domestic fowl and for a few other birds. F. A. E. Crew has reviewed these cases in two papers (*Proc. Royal Soc.*, Vol. 95, 1923, and Vol. 101, 1927).

DOG CROSSES AND HUMAN CROSSES

A Review

THIS* is the most extensive investigation ever made on the genetics of dogs. It was begun on a hunch that endocrine abnormalities might be responsible for the more or less monstrous and pathological characters of breeds of dogs having short crooked legs, or bulldog like short heads, gigantic or dwarf body size, or other peculiarities. Dr. Stockard began his studies with autopsies of "dogs of various breeds destroyed at the city pound," but this material proved unsatisfactory because of lack of information as to the age and ancestry of the animals autopsied. Through support from the Rockefeller Foundation he was enabled to establish a dog breeding farm of a magnitude never before undertaken and equipped with every device for exact and critical observational and experimental studies. Here hundreds of dogs were reared from pure bred members of many breeds, crossed in various ways. Careful records were kept of the F_1 and F_2 progeny from puppyhood to maturity, skeletons of representative individuals being saved and mounted for study after the death or destruction of the animals. The endocrines of each animal autopsied were also studied both anatomically and histologically. This was done to determine whether there was any correlation between breed peculiarities and the endocrine system. In general the results of the endocrine studies were negative or inconclusive. Size of thyroid and pituitary glands was found to vary both within breeds and between them, the conclusion being drawn that (1) "so far as influence on body form is concerned, the amount of thyroid material is not an important factor" (p. 404); (2) "gross proportional amount of thyroid is not an important factor in determining either the degree or quality of thyroid function in the dog breeds" (p. 404); (3) "although quantity of thyroid tissue . . . would seem to play no role in type determination, the relative size of the thyroid may yet be a definitely hereditary characteristic" [just as body size is].

Similar conclusions are drawn from the study of the pituitary in crosses of such diverse types as dachshund and Boston terrier, and great Dane and St. Bernard. "The large dog breeds have large pituitaries and the small toy dogs have small pituitaries. However, the weight of pituitary in milligrams per kilogram of body weight is higher in the small dogs than in the larger breeds" (p. 419). "The pituitary in the dog is not nearly so variable in size as is the thyroid, nor do the size variations of these two organs seem to be directly related. The variability of pituitary weight in the dog is about comparable to the general ratio of variability for the heart, kidney and liver, which accords in general with the findings of Brown for normal rabbits" (p. 419). In short, no evidence was found that either thyroid size or pituitary size was correlated with body type. But the possibility remained that qualitative, if not quantitative, differences might exist between the more important endocrine glands (thyroids, parathyroids and pituitaries) in different types of dogs. So careful histologic studies of these organs were made. Minor differences were found to exist between breeds but none of clear and consistent significance.

Summarizing the results of the endocrine studies based on one of the most important crosses (Boston Terrier × Dachshund) the authors say (brackets reviewer's):

> A cross between two stocks, one of which clearly possesses a defective endocrinic sys-

*CHARLES R. STOCKARD, *The genetic and endocrinic basis for differences in form and behavior*. Amer. Anat. Memoirs No. 19, 775 pp., illustr. Wistar Institute Press, 1941.

tem accompanied by distorted physical type, may give rise to a first generation of hybrids with fairly well balanced physical types and vigorous functional reactions. Individuals of this generation may even be, in some respects, physically superior to either parent stock [heterosis]. . . . The offspring from these vigorous first generation hybrids are highly heterogeneous in type [as was to be expected]; scarcely two of them are closely alike and the great majority are defective in both their morphologic quality and functional reactions. Prenatal mortality among these F_2 hybrids is high; stillbirths are common and many are viable for only a short time after birth. Harelip, cleft palate, internal hydrocephalus and other developmental arrests and defects are not uncommon in this generation. Of the members surviving to adulthood, some tend to approach in type one or the other parental stock, while others present strange mixtures and combinations of ancestral characteristics [again as was to be expected] which are in many cases incongruous and disharmonious in function. The majority of the viable members of the second hybrid generation are unstable and defective in behavior. (p. 490.)

This curious *obiter dictum* follows: "None of the results from the Boston terrier-dachshund cross offer encouragement to the indifferent attitude frequently expressed towards crossing and hybridizing the various human stocks." What human stock, it may be asked, is characterized by monstrous body form, like that of the long inbred dachshund or the Boston terrier? What occasion for alarm about the physical consequences of human crosses have we, other than the actual results of such crosses as shown by anthropological and sociological studies?

Although it was assumed by Stockard, as by others, that endocrine action is involved in the production of achondroplasic types among dogs such as the dachshund and Basset hound breeds, it was not found possible to produce a normal endocrine balance and thus restore the normal form by injections of hormones or ingrafting normal endocrine glands, a procedure which restores normal form and function in a race of hereditarily dwarf mice studied by Snell, MacDowell, and Smith.

Even if such a procedure were possible in dogs, it would still be true, as Stockard states, that the primary cause of the short-legged (dachshund) "achondroplasic" type is a gene mutation which behaves as an incomplete dominant in heredity. This same gene mutation is found in diverse association with other genes in Pekingese, where it must have arisen independently of its occurrence in European breeds.

The Genes Involved in Breed Differences

The clearest results of Stockard's experimental crosses are those which throw light on the number and nature of the gene mutations involved in the production of the breeds studied.

1. The gene for short crooked legs (achondroplasia) has already been mentioned as occurring in at least three modern breeds. It is a single factor dominant, always showing in heterozygotes but less strongly than in homozygotes.

2. A short-headed type with undershot lower jaw occurs in the English bulldog and the French bulldog. In the Pekingese and the Brussels griffon also the head is very short while the body size is very small, but the lower jaw is not markedly prognathous.

In crosses between these short-headed breeds and the dachshund, which has a normal head, the head form is intermediate in F_1 and quite variable in F_2, though without recovery of the extreme type of the short-headed parent. This indicates that more than a single gene mutation is involved in the constitution of the parental short-headed type. Little information is given about the body size of the F_2 animals, which is unfortunate, since it is quite possible that the extreme short-headedness of the Pekingese or Brussels griffon is realizable only in an individual of equally extreme small size. In dogs as in rabbits and horses (Robb) it is known that the larger the animal, the more elongated is the head form, since the normal skull grows more rapidly in its long dimension than in its short dimension, and thus becomes increasingly elongated. The same is true of ear length and leg length in rabbits.

In certain crosses of short-headed with long-headed types, as in crosses of Pekingese and Brussels griffon with Saluki

(a breed with extremely slender head and limbs) there is frequently lack of harmony in length between upper and lower jaws, resulting in both undershot and overshot mandibles. This suggests that the genes concerned with elongation of upper and lower jaws may be different, or if the same, may not act with uniform intensity, so that the jaw which develops earlier may be either longer or shorter than its mate.

Another "disharmony" according to Stockard, is manifested in crosses of the bulldog with other types and this consists in loose wrinkled skin of the head and shoulders, a character, to be sure, to be found in pure bred bulldogs and emphasized in some of the F_2 progeny, particularly those which are of large body size. Here again it is unfortunate that we are given no precise information as to the body size of the F_2 animals. For it is known that looseness of the skin, particularly on head and neck, goes with giant size, as seen for example in St. Bernard and great Dane dogs, and in the larger breeds of rabbits which regularly have a dewlap under the neck, a thing wanting in the smaller breeds of rabbits, such as Polish, which have a "tighter" skin.

3. Incidental information is supplied by the experiments of Stockard on the inheritance of differences in hair length in certain breeds. Brussels griffon is a long haired midget breed. The dachshund is a short haired breed of medium size; F_1 is long haired and F_2 shows segregation, probably into 3 long : 1 short.

Pekingese also is a long haired midget breed. Saluki has long haired ears but the body apparently is short haired. All the offspring from the cross Saluki $\times$ Pekingese both in F_1 and F_2 have long hair on the ears and moderately long hair on the body. Saluki $\times$ Basset hound (which like the dachshund has short hair) produces short haired F_1 and a segregating F_2. The long haired character of Saluki is thus shown to be less strongly dominant than that of Brussels griffon, as well as being a less developed phenotype.

4. Ear form. The German shepherd dog (police dog) has small pointed erect ears. The Basset hound has large hanging ears. When these two breeds are crossed, the F_1 animals have hanging ears of intermediate size. F_2 litters show no clear segregation of the small erect ear type, but this is occasionally recovered in a backcross to the shepherd, as shown in Stockard's plate 5, where erect ear is associated with short crooked legs. Apparently the small and erect type of ear is multifactorial, and not more than one of its constituent genes (if any) lies in the same chromosome as the crooked leg gene.

5. Screw tail of the bulldog is shown to be independent in inheritance of the bulldog head character, and to depend upon association together of two mutually independent and recessive genes. When a screw tailed bulldog is crossed with a Basset hound having a long straight tail, the F_1 animals have normal straight tails. In F_2 there is segregation into four types in a 9 : 3 : 3 : 1 ratio. The types are (1) long straight, (2) long bent, (3) short straight, and (4) short bent.

Stockard was interested primarily in the problem of development. He desired to ascertain to what extent each type of bodily structure was due to gene mutations and to what extent hormone action effected by endocrines produced the type.

His final conclusion, as nearly as it can be ascertained from his posthumously published monograph, is that gene mutations in the chromosomes are responsible for changes in body type but they may and doubtless do *act* through the agency of hormones produced in endocrine glands. In that case the character of the activity of the endocrine gland might itself be a result of gene mutation in the chromosomes.

Dogs, Men, and Rabbits

Stockard's experimental studies are a model of painstaking thoroughness, but when he allows himself to speculate beyond their scope he is less restrained. Thus he offers the suggestion, without any evidence which justifies it, that ra-

cial degeneration among humans is a necessary consequence of racial crosses. No human racial crosses have ever been made or can be made which involve gene controlled differences such as exist between short-legged and bulldog types of dogs, the reason being that such differences, though they may exist in certain families of various human races, do not characterize any race as a whole, to which category Stockard extends by implication his caution against human racial crosses. On p. 37 he says "Mongrelization among widely different human stocks has very probably caused the degradation and even the elimination of certain human groups; the extinction of several ancient stocks has apparently followed very closely the extensive absorption of alien slaves." This, of course, is pure assumption. Besides, slave making in antiquity did not involve racial diversity but only social or political status. Hence his argument involves a complete *non sequitur*. However it shows a mental bias which results in a serious misstatement of fact about rabbit crosses. On p. 22 he says: "During recent years wild stocks of rabbits have been crossed in numerous ways under domestic conditions. Some of these stocks have lately been reported by Greene, Hu and Brown ('34) of the Rockefeller Institute to give rise to structural distortions and deficiencies comparable in many ways with those known for man and the dog."

In the first place Greene, Hu and Brown did *not* in their experiments use stocks of rabbits recently wild, for the reason that no such stocks exist. All existing breeds of rabbits were derived from a single species, the European rabbit, taken into domestication at least a thousand years ago.* The Rockefeller Institute breeding experiments were made on common domestic rabbits, not "wild stocks." It has been my privilege to work with the two most striking of the "structural deficiencies" mentioned by Stockard as originated in the Rockefeller Institute experiments, namely *dwarf* and *brachydactyl*. Both are true gene mutations, recessive in inheritance, such as put in an appearance when a race of animals is inbred so as to uncover them. There is no necessary antecedent period of racial crossing in rabbits or in other domestic animals, such as rats, mice, guinea-pigs, cattle and horses, before gene mutation occurs. It would be more correct to state that inbreeding, rather than outcrossing, occasioned the appearance of these degenerative changes. But their causation is not to be ascribed to either process but to spontaneous gene mutation.

An attempt was made some years ago by Mjoen to show by experimental evidence that crossing different breeds of rabbits results in physical degeneracy and that consequently Norwegians should not mix with Lapps. Mjoen's experiments have been reviewed elsewhere† and his conclusions so far as rabbits are concerned completely disproved. It is unfortunate that Stockard should have introduced into his dog experiments similar *non sequiturs* as to the implication of his experiments on human race problems.

W. E. Castle

University of California

*Castle, W E. *Am. Nat.* 59:280. 1925.
†Castle, W. E. *Jour. Hered.* 15:363. 1924.

AN AMPHIDIPLOID *LACTUCA*

Produced through Non-Reduction in F_1 Hybrids

ROSS C. THOMPSON

Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture

THE material presented in this paper was obtained as an outgrowth of studies undertaken by the Bureau of Plant Industry of the U. S. Department of Agriculture to locate hereditary factors in lettuce for resistance to the aster-yellow virus. After a comprehensive study of many varieties of garden lettuce it was concluded that no resistance of value in breeding is present in the cultivated form *Lactuca sativa*. Attention was then turned to wild species of the genus. Studies were made on 18 species collected from both domestic and foreign sources. Many crosses were made and numerous interspecific hybrids obtained in determining the possible value of certain of these wild species in breeding for disease resistance in cultivated lettuce. The amphidiploid form herein described was discovered in one of these interspecific hybrid populations.

In two former papers Thompson, Whitaker and Kosar[8] and Whitaker and Thompson[10] have reported their findings regarding certain genetic relationships among species of the genus *Lactuca*. The 18 species studied included two 8-chromosome, twelve 9-chromosome and four 17-chromosome species. Fifteen of the 18 species were found by their breeding behavior to fall into three compatibility groups. The results reported indicate two compatibility groups for the 9-chromosome species and one group for the 17-chromosome species. No close relationships were reported for the 8-chromosome species studied. It is generally assumed that the 17-chromosome species have arisen as amphidiploids from crosses between 8- and 9-chromosome species. The present paper presents evidence in support of the amphidiploid origin of the 17-chromosome species found in nature and describes the mechanism through which the 17-chromosome species may have come into existence.

The three compatibility groups include the following species:

Group 1, the *Serriola*-like (*Scariola*) species, *Lactuca serriola* L., *L. virosa* L., *L. saligna* L., *L. altaica* Fisch and Mey. *L. virosa* L. and the cultivated form *L. sativa* L.

Group 2, *L. indica* L., *L. laciniata* (Houtt.) Makino., *L. raddeana* Maxim., *L. tatarica* (L.) C. G. Mey., and closely related species.

Group 3, the four 17-chromosome species *L. canadensis* L., *L. spicata* (Lam.) Hitchc., *L. graminifolia* Michx., and *L. floridana* (L.) Gaertn.

The 9-chromosome species in Group 1 were found to be almost completely incompatible with species in either of the other Groups. The 9-chromosome species in Group 2 were found to be closely related among themselves and to certain species in the 17-chromosome Group 3. The four 17-chromosome species in Group 3 showed close relationships among themselves and with certain of the species in Group 2.

Viable seeds were obtained from 16 crosses between species having 9 and 17 chromosomes, respectively. In all but two of the 16 crosses, the hybrid plants failed to produce seed. In many cases the hybrid seedlings were very abnormal and died in early stages of development. In two crosses, *Lactuca spicata* ($N = 17$) $\times$ *L. indica* ($N = 9$) and *L. graminifolia* ($N = 17$) $\times$ *L. indica* ($N =$

*The writer wishes to acknowledge his indebtedness to Dr. Haig Dermen of this Department for many helpful suggestions.

SEEDS OF PARENT SPECIES AND OF HYBRIDS

Figure 5

Size of seed is one of the few characters in which the hybrid exceeded either parent. Most characteristics were intermediate in the hybrid. *L. spicata* was the female parent in this cross.

9) the F_1 hybrids were vigorous plants. While almost sterile, some seeds were produced.

The life history of one of these two partially fertile hybrids, *Lactuca spicata* × *L. indica,* has been studied in detail and the results are the basis for this paper.

Materials and Methods

The parent seed of *Lactuca spicata* was collected by the writer near Skyland Drive in Shenandoah National Park, Va. The seed of *L. indica* was obtained from G. L. Stebbins, Jr., University of California, who indicated it to have come from a Chinese source.

The parent plants were grown in 10-inch clay pots in a screened greenhouse at Beltsville, Md. In July, 1939, a number of heads of *Lactuca spicata* were depollinated with water. Pollen from flowers of *L. indica* was applied to the washed heads of *L. spicata.* From these crosses a number of seeds were obtained from which plants were grown. Fifteen of these plants from this seed were hybrids, as proved at an early stage by the red pigmentation of the leaves, a dominant character.[9]

Flower heads from both F_1 and F_2 plants were preserved for cytological study of sporogenesis by killing in a 3 to 1 absolute alcohol-acetic acid mixture, and storing in 75 per cent alcohol.

The cytological studies and the photomicrographs presented were all made from preparations made by the iron-aceto-carmine smear technique. In some cases where it was desired that the cytoplasm be stained for photographic purposes a little hematoxylin was added to the stain solution.

The photomicrographs (except Figure 7*K*) were taken with a Spencer microscope using 20× and 44× objectives and 25× and 30× oculars. A Bausch and Lomb "Type K" camera was used throughout. Figure 7*K* was taken with a Zeiss microscope using 60× objective and 20× ocular.

Results

Description of F_1 Plants

The F_1 *Lactuca spicata* × *L. indica* hybrids were typical for first-generation hybrids in that they were in many characteristics intermediate between the two parent species. In height the hybrids were taller and had heavier stems than *L. indica,* but they were much shorter and more slender than *L. spicata.* Under similar field conditions *L. indica* plants averaged about three feet, *L. spicata* about ten feet and the F_1 hybrids near five feet. Lateral branching in the hybrids extended well down on the stem as in *L. indica,* in contrast to the more terminal branching of *L. spicata.*

The leaves of the F_1 hybrids were broader and thicker than either parent and had deep runcinate lobes. The hybrids had red pigmented leaves as is true of *L. indica,* whereas *L. spicata* is free from red pigment in its leaves. In *L. indica* the red pigment is confined to small scattered areas that give a spotted effect while in the hybrids the pigmented areas are very much larger, covering almost all of the leaf surface. For a com-

parison of the rosette leaves of the hybrid with its parents see Thompson, Whitaker and Kosar[8] Plate 3*E*.

The flowers of the F_1 hybrids were intermediate as to size of head, but the number of florets per head was greater than either parent. Both parent species and the resulting hybrids have yellow flowers.

Of a population of 15 F_1 hybrid plants obtained from this cross, ten were grown to maturity in the greenhouse and five were grown in the field at Beltsville, Md. Every one of the ten greenhouse-grown plants was completely sterile and not a seed was obtained. Of the five field-grown F_1 plants two were completely sterile, two produced a few seeds, and one yielded several hundred seeds.

The difference in behavior of the greenhouse- and field-grown plants with respect to degree of sterility is believed to be at least partially due to environmental conditions. The temperature in the greenhouse during the period when the inside-grown plants were maturing often reached the high nineties during the hottest portion of the day. During some very hot days the maximum temperature in the house exceeded 100° F. The temperature in the field during the same period averaged 10 or more degrees lower. Observations made during the progress of these studies as well as many other investigations dealing with *Lactuca* hybrids indicate that very high temperatures (90° F. or above) have a detrimental effect on seed-setting. Hybrids from the same parent species have frequently yielded seeds if the temperature was moderate during the maturity period, while no seeds set when the plants reached maturity during a period of very high temperature.

Size of seeds differed from most other hybrid characters in that the seeds were larger than those of either parent and not intermediate. The hybrid seeds have the thin outer margin and long narrow beak typical of *L. indica,* but the beak is approximately twice as long as in *L. indica* seeds, and the hybrid seeds are much larger. Seeds of the two parent species and the F_2 hybrid are shown in Figure 5.

F_2 Generation

All of the F_2 plants grown were from the one field-grown F_1 plant that yielded the largest amount of seed. Absence of the expected F_2 segregation was observed very early in the development of the F_2 population. All of the plants were of a uniform type, giving the population the appearance of a fixed species. It was this striking characteristic of the F_2 population that called our special attention to this hybrid and led to the cytological study.

Environmental conditions, light relations in particular, have a very marked effect on the morphology of plants of the genus *Lactuca.* Morphological differences resulting from variations in growing conditions tend to make comparisons difficult. Since the F_1 and F_2 plants were not grown under the same conditions, any comparisons are likely to be in some degree erroneous. In general the F_2 plants grown in the field in the summer of 1941 looked very much like the F_1 plants grown in the open in 1940. One striking difference in the two lots of plants was the thicker, coarser leaves of the F_2 plants, especially in the rosette stage. Other than this the two lots of plants appeared similar. Some of the differences in foliage of the F_1 and F_2 plants are indicated in Figure 6.

Cytological Observations

Root-tip Studies

Chromosome counts made from root-tip smears stained with iron-aceto-carmine showed the F_1 somatic number to be 26. No preparation was obtained in which it was possible to make an exact count of the somatic number in the F_2 material. In the latter preparations as many as 48 chromosomes could frequently be counted. It was certain from the observations made that the somatic chromosome number of the F_2 root tips was near 52 .

Observations on the F_1 Meiosis

In the microsporocytes of the F_1 many irregularities were observed. Irregularities were found at both meiotic divisions. In many cases synapsis was partial and both bivalents and univalents were pres-

LEAVES OF F_1 AND F_2 PLANTS

Figure 6

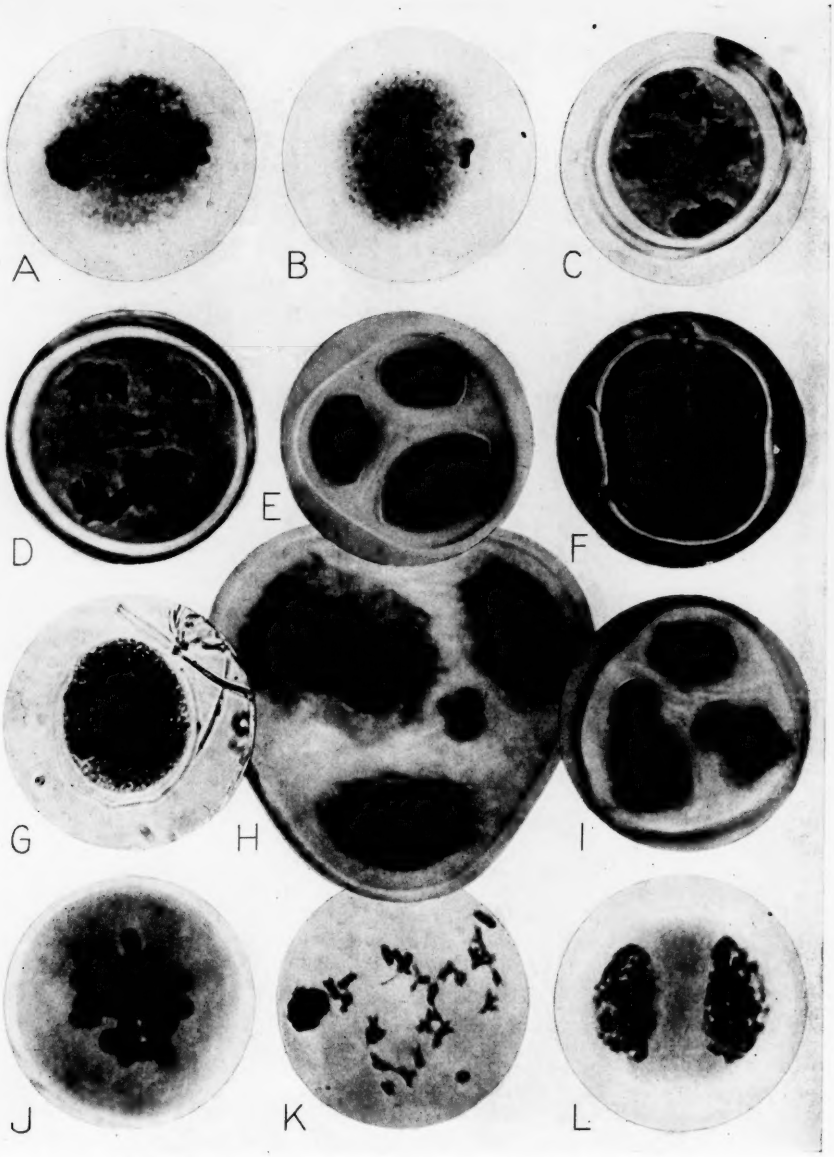
The F_2 plants (*B*) grown from an F_1 plant of the *spicata* × *indica* hybrid showed no segregation and were remarkably uniform. The leaves of the F_2 were larger and more fleshy than of the F_1. This behavior gave a hint that the chromosome constitution of the hybrid was unusual.

ent at diakinesis. The most common pairing relationship observed was seven univalents, eight bivalents and one trivalent. One trivalent of three approximately equal-sized chromosomes joined end-to-end was present in most cells satisfactory for the observation of pairing relationships. It was not possible from the limited material available to determine the behavior of the univalents at anaphase.

Frequently one or two pairs of chromosomes (and sometimes three pairs) appeared to be lost in the cytoplasm at late anaphase. In many cases tetrads formed which appeared to be normal (Figure 7*F*). The pollen grains from these tetrads were apparently fertile* as indicated by iron-aceto-carmine staining of the pollen.

Lagging chromosomes were observed at both divisions. Lagging at the first division is shown in Figure 7*A* and *B*. At the second division lagging was

*Fertility of pollen, as used throughout this discussion, refers to pollen grains that became darkly stained with iron-aceto-carmine in contrast to aborted pollen grains that remained unstained or only faintly colored.



MICROSPOROCYTES OF FIRST GENERATION HYBRIDS

Figure 7

Chromosome behavior in microsporocytes of F_1 generation hybrids of *Lactuca spicata* × *L. indica*. *A* and *B*—Lagging chromosomes at first anaphase resulting from partial pairing at first meiotic metaphase. *C*—Second meiotic late anaphase (lagging chromosomes in one of the two dividing nuclei). *D*—Second meiotic anaphase (lagging in both dividing nuclei). *E*—A tryad microsporocyte resulting from failure of one of the two nuclei to divide at the second division. Note the one very large and two smaller equal sized microspores. *F*—A tetrad in which the microspores appear to be normal. This type of microsporocyte may give rise to the smaller fertile type of pollen grains. *G*—A microsporocyte that may result in polyspory. Microsporocytes of this kind resulted when there were chromosome aberrations in both meiotic divisions. *H* and *I*—Pentads, a very frequently observed form of polyspory. Note the small nucleus in the cytoplasm of the most central of the four large spores in the pentad shown in *H*. *J*—A typical asynaptic first metaphase showing the 26 univalent chromosomes massed at the center of the cell. *K*—Homotypic division of an unreduced nucleus showing the 26 univalent chromosomes dividing longitudinally. *L*—Dyad nuclei which will result in diploid pollen grains. *A*, *B*, *C*, *E*, *F*, *G*, and I, × 917; *K*, × 1000; *D*, *J*, and *L*, × 1100; and *H*, × 1500.

sometimes observed in only one of the two dividing nuclei (Figure 7*C*). In some cases there was lagging in both dividing nuclei (Figure 7*D*). Failure of one of the two nuclei to divide at the second division resulted in triads of the type shown in Figure 7*E*, having one large and two smaller microspores.

Aberrations in microsporogenesis in the F_1 generation resulted in many types of spores. Microsporocytes were observed having from two to eight spores, one or more of which often had small nuclei scattered in the cytoplasm (Figure 7*G*, *H*, and *I*). A small nucleus in the cytoplasm of a large spore may be seen in the most central of the four large spores in the pentad shown in Figure 7*H*.

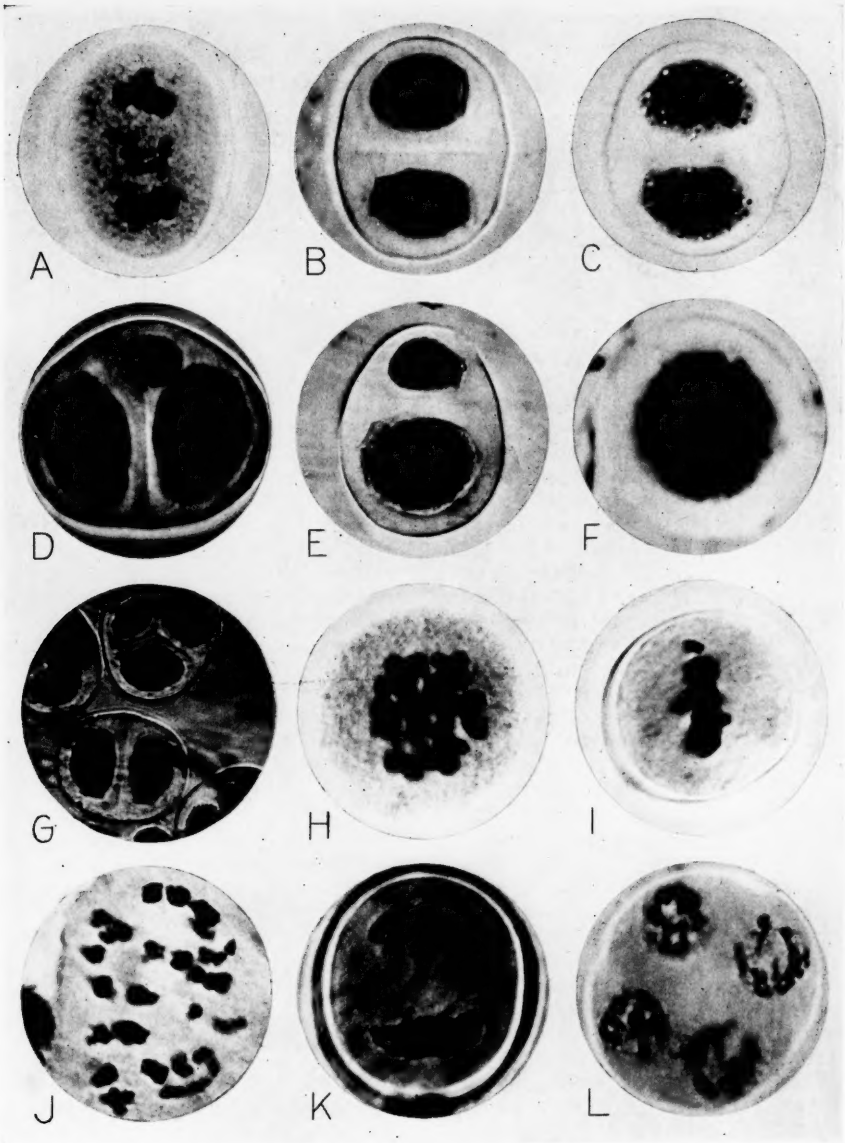
Partial pairing did not occur in all microsporocytes. In a predominating number of sporocytes complete absence of pairing was the rule. Complete asynapsis at the first meiotic division resulted in the formation of a single large nucleus arising by failure of the first division in a manner similar to the genesis of the "restitution nucleus" reported by Rosenberg[6] as occurring in the meiosis of certain parthenogenetic forms of *Hieracium*. A typical asynaptic metaphase in polar view is shown in Figure 7*J*. That these large cells had the unreduced number of 26 chromosomes was proven by the presence of 26 univalent chromosomes dividing homotypically, presumably at the second metaphase, Figure 7*K*. Thus, following the failure of the first division, the large cell went into interphase. At the second division the chromosomes split longitudinally and dyads resulted, each having 26 chromosomes, 17 from *Lactuca spicata* and 9 from *L. indica*.

The division of the unreduced nucleus appeared in most cases to be regular, as indicated by the late telophase shown in Figure 7*L*. Normal dyads as indicated in Figure 8*B* usually resulted from the division of the unreduced nucleus. However, the division of the unreduced nucleus was not in every case regular and several types of abnormal microspores developed as the result of abnormal divisions. In some mounts of microspore material, various numbers of chromosomes were seen to remain at the equatorial position at anaphase in the division of the unreduced nucleus (Figure 8*A*). Various kinds of triads generally resulted (Figure 8*D*). Small nuclei in the cytoplasm of one or both of the dyad microspores frequently resulted from lagging at division of the unreduced nucleus (Figure 8*C*). A few dyads were observed having microspores of very unequal size, as shown in Figure 8*E*. The differences in size of the two spores were in some cases much greater than indicated in this figure. It is possible that in some cases spindle formation also failed completely at the second division so that a giant microspore having 52 chromosomes developed. Figure 8*F* shows a giant microspore in which exine can be seen to be forming around the one large nucleus. Kagawa[2] suggested that such polyploid spores may arise through failure of division of the unreduced nucleus in which all of the chromosomes stay together. He presented a camera lucida drawing of an unreduced nucleus in a *Triticum-Aegilops* hybrid in which all of the chromosomes stayed together and a single giant microspore resulted. Further evidence that the same phenomena occur in *Lactuca* hybrids is presented in the discussion of the pollen studies.

A portion of a smear preparation from an F_1 flower in which dyads, triads, and tetrads all lay side by side is shown in Figure 8*G*.

Observations on the F_2 Meiosis

Examination of F_2 material indicated 26 pairs of chromosomes at early first metaphase (Figure 8*J*). In most microsporocytes, meiosis appeared to be regular (Figure 8*K* and *L*). Although most of the meiotic divisions in the F_2 microsporocytes appeared to be normal with tetrads resulting (Figure 9*A* and *C*), many of the irregularities observed in the F_1 meioses were present in very limited degree. Some of the F_2 meiotic irregularities are shown in Figure 9*B* and *D*). Lagging of chromosomes at the



FORMATION OF F_1 AND F_2 POLLEN GRAINS

Figure 8

Chromosome behavior in microsporocytes of F_1 and F_2 generation hybrids from the cross *Lactuca spicata* × *L. indica*. *A*—Lagging chromosomes at homotypic division of an unreduced nucleus. A triad like that shown in *D* results from such an abnormal division of the unreduced nucleus. *B*—A dyad microsporocyte resulting from homotypic division of an unreduced nucleus. *C*—A microsporocyte resulting from abnormal division of an unreduced nucleus. Note small nuclei in the cytoplasm of both microspores. *D*—A triad microsporocyte resulting from abnormal division of an unreduced nucelus as indicated in *A*. *E*—A dyad microsporocyte in which abnormal division of an unreduced nucleus resulted in two microspores of very unequal size. *F*—An F_1 microsporocyte in which both meiotic divisions failed and a single giant pollen grain developed. *G*—A section of a smear preparation in which dyads, triads, and tetrads lay side by side. *H* and *I*—Typical first metaphases in polar and equatorial views of F_2 microsporocytes. *J*—First metaphase showing the 26 bivalent chromosomes in an F_2 microsporocyte; *K*—A typical first division in an F_2 microsporocyte. *L*—Tetrad stage following second division in an F_2 microsporocyte. *G*, × 500; *A*, *B*, *C*, and *E*, × 917; *D*, *F*, *H*, *I*, *J*, *K*, and *L*, × 1100.

first division (Figure 9*B*) was occasionally observed. Although lagging chromosomes in both dividing nuclei at the second division (Figure 9*D*) were present in some cases, true polyspory was rarely observed in the F_2 meiosis. Supernumerary nuclei resulting from lagging chromosomes were occasionally observed in the cytoplasm of some of the F_2 microsporocytes.

In two mounts of F_2 microsporocytes some dyads were observed (Figure 9*E*). Careful study of many other mounts of similar material failed to show dyads. As will be shown later, studies on the F_2 pollen indicated that dyads were also formed in the F_2 microsporogenesis. This is a point that should be given further study. It is possible that more complex polyploids might have appeared in a larger progeny.

Observations on the F_1 Pollen Grains

Examination of pollen grains stained with iron-aceto-carmine showed great variation in size and fertility. Counts of 1,000 pollen grains from each of three F_1 plants gave 6.5, 13.0 and 93.6 per cent of fertile grains, respectively. These fertility counts were all made from plants that were fully sterile. Some of the pollen grain types are shown in Figure 9*H-K*. Three sizes of fertile pollen grains were present, as indicated by deep staining. There were many sizes of aborted pollen grains that failed to stain, varying from very small ones to others almost as large as the largest stained pollen grains. Some of the types of aborted pollen grains are shown in Figure 9*H* and can be distinguished by their very light color, as compared with the fertile ones. Three of the smaller-sized fertile pollen grains and one of the medium-sized fertile grains are shown in Figure 9*H*, and one giant grain is shown in Figure 9*I*.

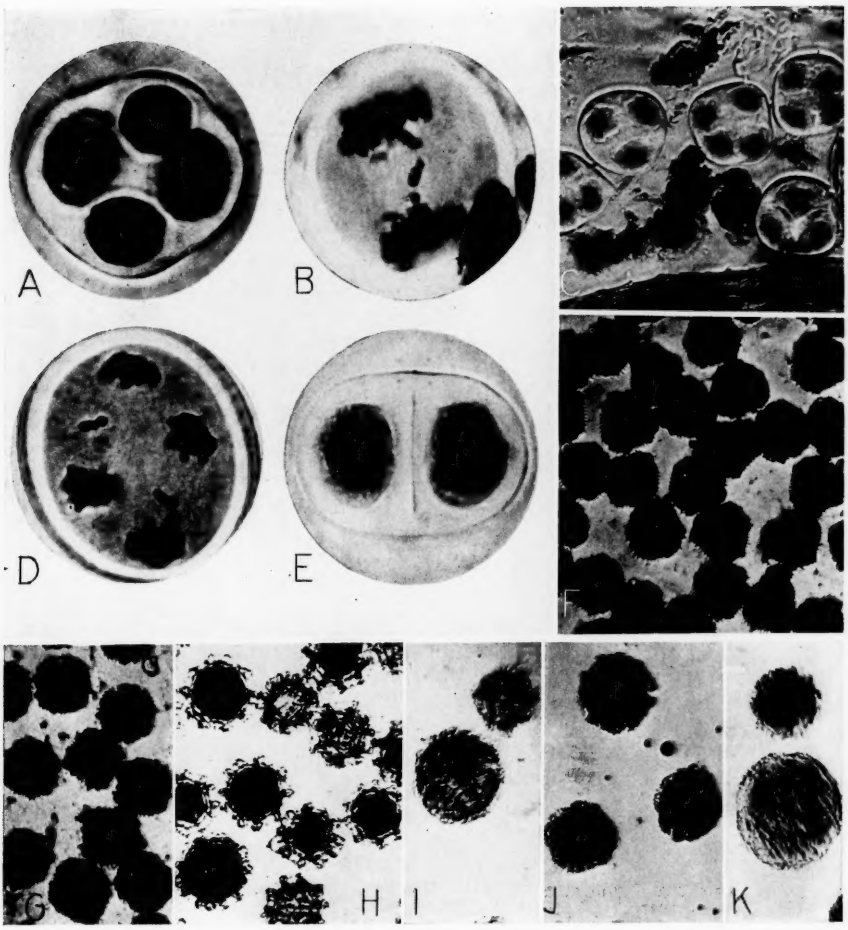
Pollen grains of the parent species *Lactuca spicata* and *L. indica* are shown in Figure 9*F-G*, respectively. The photographs in Figure 9*F-K* are of equal magnification so that comparisons of pollen grain size can be made. The pollen grains of *L. indica* averaged a little larger than the pollen grains of *L. spicata*. The smallest pollen grains of the F_1 hybrids were approximately the size of the *L. indica* grains. The middle-sized pollen grains were larger than in either parent and were present in much greater numbers than the other two fertile types. The smaller pollen grains were quite numerous in some mounts. The giant type pollen grains, Figure 9*I*, were very few in number and never developed the heavy exine characteristic of the two smaller types.

The smaller-sized fertile F_1 pollen grains apparently developed from those microsporocytes in which partial pairing at the first meiotic division resulted in some tetrads that appeared to be normal in every way. Dyad microsporocytes from unreduced nuclei were present in much greater numbers than other types of spores and gave rise to larger pollen grains than the tetrads. Since the middle-sized pollen grains were present in much greater numbers than the other sizes of fertile pollen grains, it seems reasonable to assume that they were of dyad origin. The few giant pollen grains are believed to have developed from unreduced nuclei in which none of the chromosomes separated at the second division. This seems likely in view of the very unequal dyads observed (Figure 8*E*); and the observations of Kagawa[2] in *Triticum-Aegilops* hybrids lend support to this conclusion. An interesting observation in this connection was that all of the pollen grains of a larger size than the middle-sized fertile pollen grains had thin walls. Most of these were aborted and only the very largest ones gave the deep stain reaction indicating fertility.

Observations on the F_2 Pollen Grains

Stain tests made on F_2 pollen grains indicated practically all of the pollen to be fertile. A few non-staining pollen grains were usually present and their number appeared to be much greater in material killed during very warm weather.

Examination of the deeply stained fertile F_2 pollen grains indicated two sizes



POLLEN GRAINS OF HYBRIDS

Figure 9

Pollen formation in F_2 hybrids of *Lactuca spicata* × *L. indica*. *A* and *C*—F_2 tetrads. The apparent triads are due to the plane in which they are photographed. *B*—Lagging chromosomes at first division in an F_2 microsporocyte. *D*—Lagging at second division in F_2 microsporocyte. *E*—Dyad from an F_2 microsporocyte. *F*—Pollen grains of *Lactuca spicata*. *G*—Pollen grains of *L. indica*. *H* and *I*— Pollen grains of F_1 *L. spicata* × *L. indica hybrids*. Note the three sizes of fertile pollen grains. *J* and *K*—F_2 hybrid pollen grains (showing two sizes of fertile grains). *A*, *B*, *D*, and *E*, × 1200; *C*, × 420; *F*, *G*, *H*, *I*, *J*, and *K*, × 250.

(Figure 9*J* and *K*). The majority were of the size shown in Figure 9*J*, but a few very large thin walled pollen grains like the large one in Figure 9*K* were observed. These giant pollen grains are very likely the result of dyads, two of which were observed in studies of microsporogenesis in the F_2 generation.

Discussion

That polyploid species in plants might arise from chromosome doubling in the

zygote following hybridization has been emphasized by Winge.[11] For some years following his report, the doubling of chromosomes in the zygote soon after fertilization was held to be the most likely method by which polyploid species had been developed in nature.

The production of polyploid species through non-reduction of chromosomes at the first meiotic division followed by fertilization between the diploid gametes was recorded in the report of Karpechenko[3] on polyploids from *Raphanus-Brassica* hybrids. Since Karpechenko's report in 1924, several authentic cases of polyploids arising from fertilization of unreduced gametes have been reported, in *Digitalis* by Buxton and Newton,[1] in *Nicotiana* by Rybin[7] and by Lammerts,[5] and in *Aegilops-Triticum* hybrids by Kihara and Katayama.[4] Polyploids in nature may have arisen through fertilization of unreduced gametes as well as from doubling in the zygote. The cases of constant forms of polyploidy through hybridization have been summarized by Winge.[12]

To our knowledge this present report is the first to be made on constant polyploids in *Lactuca,* arising through fertilization of unreduced gametes.

In the *Lactuca* hybrids the F_2 plants were partially fertile, which condition has resulted in the establishment of a true-breeding 26-chromosome amphidiploid form. Since this new amphidiploid was derived from the chromosome complements of *Lactuca spicata* and *L. indica* it is here suggested that the new form be designated as *Lactuca indicata.*

The new amphidiploid form is not fully fertile. In a population of the F_2, grown in a greenhouse at Beltsville, Md., in the spring of 1941 when temperature and light relations were favorable, from 50 to 60 per cent of the ovules developed viable seeds. The number of seeds set per head varied from one to, in a few cases, 15 or more. All of the seeds that developed were large and plump and nearly all of them germinated. In a population of F_2 plants, grown in the greenhouse during the summer of 1941, the percentage of ovules producing seeds was not more than 10 to 15 per cent. Since both populations were grown from the same lot of F_2 seeds, it is apparent that the unfavorable high temperature or some other environmental factor was responsible for the reduction in seed production in the second planting. Cytological examination of meiotic divisions in material from both plantings indicated that there were more aberrant divisions in the material preserved from plants maturing during very warm weather.

The common occurrence of nine chromosome associations at meiosis in the F_1 hybrids indicates that the 17-chromosome species *Lactuca spicata* is very likely an amphidiploid.

That fertility of pollen as indicated by staining is not of great value in determining the capacity of a plant to set seed is shown by pollen fertility counts given for three of the F_1 hybrid plants. These three greenhouse-grown plants showed fertility counts, on a basis of staining, of 6.5, 13.0 and 93.6, respectively. Nevertheless, all three of these plants were fully self-sterile.

Since the amphidiploid form was obtained from seed of the field-grown F_1 plant producing the most seed, it might be questioned whether this plant was itself an amphidiploid, having originated through chromosome doubling in the zygote. It is also possible that the seeds obtained from this plant were from laterals or from sectors of the plant that were actually amphidiploid through some localized doubling of the chromosomes. The failure of forms having other than 26 somatic chromosomes to appear in the F_2 is also without an explanation. This may be advanced as evidence that the new amphidiploid form arose through somatic doubling rather than through fertilization between unreduced gametes.

Since the 15 F_1 plants all appeared to be very much alike, no attempt was made to obtain root tip counts on all 15 plants. If any striking differences had been observed among these plants an effort would have been made to study root tips from the various types present. It was much more convenient to obtain root tip

material from the 10 plants grown in the greenhouse than from the field-grown plants; consequently all of the material preserved was taken from greenhouse plants and all of these indicated 26 somatic chromosomes. However, all of the 15 plants were carefully observed for variations before five of them were transplanted to the field. A few F_1 seed had been saved for treating with colchicine and these were germinated several months later.

In the colchicine treated lot were a number of plants that showed no indication of colchicine effect. Some of these were still in the rosette stage at the time the first F_2 population was being grown from the most fertile field-grown F_1 plants. This afforded the opportunity to photograph typical F_1 leaves with typical leaves from the F_2 amphidiploid. The larger, thicker, coarser leaves of the F_2 plants are shown in Figure 6. This illustration shows clearly the difference in the morphology of the leaves of the two generations from this cross. This is evidence that there was some marked difference in the constitution of the F_1 and F_2 plants, and points to chromosome doubling through fertilization between unreduced gametes rather than through some form of somatic doubling.

That the new form did not arise through amphidiploid sectors of the F_1 is evidenced by the fact that the seeds produced on all three of the seed-producing hybrids were harvested at random from all parts of the plant. The fruiting heads were not localized in parts of any of the three plants as would be the case if seeds were produced only on amphidiploid sectors.

There is no satisfactory explanation for the fact that plants with other than 26 chromosomes do not appear in the F_2. In some mounts dyads constituted as much as 40 per cent of all microsporocytes. Since most if not all of these should be stable and capable of functioning the chances for progenies from them should be greater than from other types of microspores, providing dyad megaspores are produced in the same proportion. Since the tetrad microspores probably resulted from a *Drosera* type of pairing, only a small proportion of these might be expected to be stable and capable of producing progenies. However, a small percentage of these should produce stable and functional 9- and 17-chromosome gametes. It is not clear why progenies from these have not been found.

Summary

Out of 16 crosses made between 9- and 17-chromosome species in the genus *Lactuca* two gave partially fertile F_2 progenies.

The life history of one of these hybrids, obtained by crossing *Lactuca spicata* ($n = 17$) with *L. indica* ($n = 9$) was studied in detail. Lack of segregation among the F_2 plants and the development of thick, coarse leaves suggested some form of polyploidy.

Detailed cytological examination of the F_1 root tips and of microsporogenesis in the F_2 plants revealed that these are amphidiploids having 26 pairs of somatic chromosomes. In an F_2 population of 127 plants there was no evident segregation. All of the plants appeared to be identical and looked like plants of a fixed species.

Cytologically the microsporogenesis of the F_1 plants showed that spores developed from three types of chromosome behavior: (1) Partial pairing with various numbers of bivalents and univalents, frequently 1 trivalent, 8 bivalents and 7 univalents. In some of these cases of partial pairing, fertile pollen grains apparently developed. (2) Asynapsis with failure of the first meiotic division, resulting in the formation of a large unreduced nucleus. The second division resulted in dyads and in the formation of fertile pollen grains having the unreduced number of 26 chromosomes. (3) Failure of both first and second meiotic divisions, resulting in the development of a single giant pollen grain which was assumed to have 52 chromosomes.

Although no study was made of F_1 megasporegenesis it is apparent that the reduction division must also have failed in genesis of the female gametophyte.

Since only plants having a haploid number of 26 chromosomes appeared in the F_2 population, all of the plants must have developed from the union of unreduced gametes. The other types of gametes described did not function.

Literature Cited

1. Buxton, B. H., and W. C. T. Newton. *Jour. of Gen.* 19:269. 1928.
2. Kagawa, F. *Jap. Jour. Bot.* 4:345-361. 1929.
3. Karpechenko, G. D. *Jour. of Gen.* 15: 375. 1924.
4. Kihara, H., and Y. Katayama. *Cytologia 2*:234. 1931.
5. Lammerts, W. E. *Genetics* 16:191. 1931.
6. Rosenberg, O. *Svensk. Bot. Tidskr.* 11: 145-206. 1917.
7. Rybin, W. *Ibid.* 47:385. 1929.
8. Thompson, R. C., T. W. Whitaker, and W F. Kosar. *Jour. Agr. Res.* 63:91-107. 1941.
9. Thompson, R. C. *U. S. D. A. Tech. Bul. 620.* 37 pages. 1938.
10. Whitaker, T. W., and R. C. Thompson. *Bul. Torrey Bot. Club* 68:388-394. 1941.
11. Winge, C. R. *Trav. Carlsb.* 13:131-275. 1917.
12. ————————. *Svensk. Bot. Tidskr. 26*:107-122. 1932.

✦

Plant Breeding — The Modern Way

IN times such as these, when paper is scarce and everybody is supposedly very busy, book reviewers might provide about as much accurate information as heretofore in much less space. For example, the reviewer might say regarding this volume,* that Professors Hayes and Immer are unquestionably recognized authorities in this field; that the University they are connected with is one of the prominent ones along agricultural lines; that its Division of Agronomy and Plant Genetics has a fine record of successful accomplishment and prominent students; that the paper, format, and printing of the book are excellent, and finally, that the publishing company is one of the best.

About all I can add to this is that I think it is a good book for agricultural students and for courses in plant breeding, its chief omissions being special chapters on cotton, peanuts, and sorghums and a set of problems. The addition of the former would broaden its territorial usefulness and the addition of problems at the chapter endings would teach its readers conciseness in thinking, speaking, and discussing this subject, of which there is a deplorable lack at present, even among mature biologists.

It might also be added that the book stresses practical breeding, particularly as regards diseases and insect resistance, and such crops as corn, oats, barley, wheat, and flax. There is an excellent glossary and bibliography.

Orland E. White
The Blandy Experimental Farm, University of Virginia.

✦

Meeting of Scientific Photographers

The Biological Photographic Association will hold its twelfth annual Convention in New York City September 10th, 11th and 12th. Present-day methods of obtaining photographs for teaching and scientific records will be discussed in detail. Particular emphasis will be placed on the types of photographs needed in the present emergency. The Convention Chairman will be Mr. Joseph Haulenbeek, Illustration Bureau, Rockefeller Institute for Medical Research, New York City. Further particulars about the meeting and the program may be had by writing him.

The Biological Photographic Association is a national, non-profit organization, formed to act as a clearing house for information on the methods of scientific illustration. Its members are scientific photographers, scientists interested in the application of photography to their fields, and the makers of precision photographic equipment. Information on various techniques, collected from experienced workers all over the country, is dispensed by means of the Association's Quarterly Journal.

*H. K. Hayes and F. R. Immer. Methods of Plant Breeding. Pp. 432 + xii. Cloth Bound $4.00. McGraw-Hill, N. Y. 1942.

THE PATTERN OF SALIVARY GLAND CHROMOSOMES

In a Hybrid in the Genus Chironomus

ELIZABETH GOLDSCHMIDT
*Department of Zoology The Hebrew University Jerusalem**

WILD populations of Chironomids have been investigated by Bauer,[3] and Dubinin, Sokolov and Tiniakov.[9] In each case the occurrence of chromosome abnormalities was found to be high, inversions being by far the most frequent type of aberration. Bauer investigated the cytological features of 16 species of Chironominae and found numerous correspondences in the general caryotype as well as in details of banding. The present investigation was carried out with the object of comparing the salivary chromosome patterns of nearly related strains of the genus *Chironomus* as has been done with other Dipteran genera (*Drosophila, Sciara*).

Two undetermined strains of *Chironomus* from different localities in Palestine were crossed, mass matings being made between females of strain *A* and males of strain *B*. The resulting batches of eggs yielded a viable F_1. The reciprocal cross has not yet been carried out. The hybrid F_1 males were back-crossed to females of the maternal strain and vast numbers of normal offspring were obtained. The F_1 hybrids were also fertile *inter se* and produced a normal F_2 generation. From these a normal F_3 was obtained.

In the absence of standards, no exact estimation of fertility and viability could be made in any of these crosses, but neither the number nor the vigor of the individuals seemed to be reduced as compared with normal wild types. This apparently complete fertility would seem to indicate a very close relationship between the paternal strains. However, cytological examination revealed a large discrepancy in the salivary pattern.

All investigations were carried out on smear preparations fixed and stained in the usual manner in acetocarmine. The preparations were transferred through 96 per cent alcohol into Venetian turpentine and thus made permanent, according to the method of Bauer[2] and Geitler.[10]

In all general features the chromosomes of both strains conform to the description given by Bauer of *Chironomus thummi*. There are three long chromosomes of approximately equal lengths (I, II, III) and one small chromosome (IV), whose length is about a quarter of that of the long chromosomes. There is no central magma but the chromosomes appear in the smears independent of each other (Bibiotype), the bulk of the nucleolar mass being associated with chromosome IV. Synapsis between partners is very close in the normal wild type nucleus of both strains. It may occasionally be interrupted at one end of chromosome IV.

Preliminary chromosome maps of the three long chromosomes were compiled from a number of camera lucida drawings.† With the aid of these maps pairing conditions in the hybrid were in-

*This work was carried out in the Department of Zoology of the Hebrew University, Jerusalem, under the supervision of Dr. Georg Haas to whom my sincerest thanks are due for his constant help and advice. I also wish to thank Miss B. Malachowski who took the photos in the Cancer Laboratories by kind permission of Dr. Doljanski.

†These maps, as well as a number of photographs of chromosomes not published with this paper, are deposited in the American Documentation Service. They may be obtained from the nonprofit Bibliofilm Service, 1719 N St., N. W., Washington, D. C., by ordering Document 1640, remitting 25 cents for copy in microfilm, readably enlarged full-size on reading machine or hand viewer, or 60 cents for copy in the form of paper photoprints readable without optical aid.

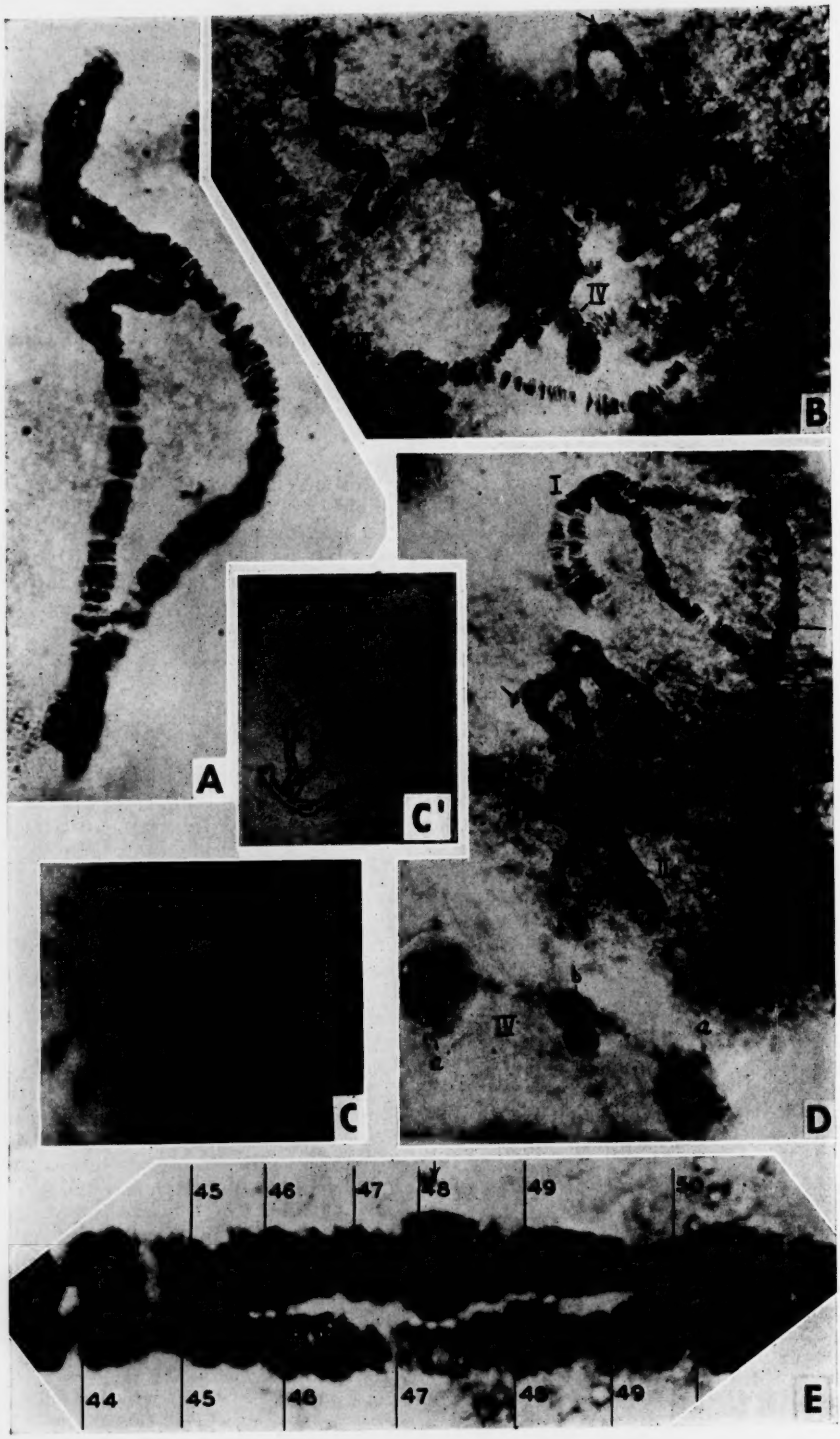
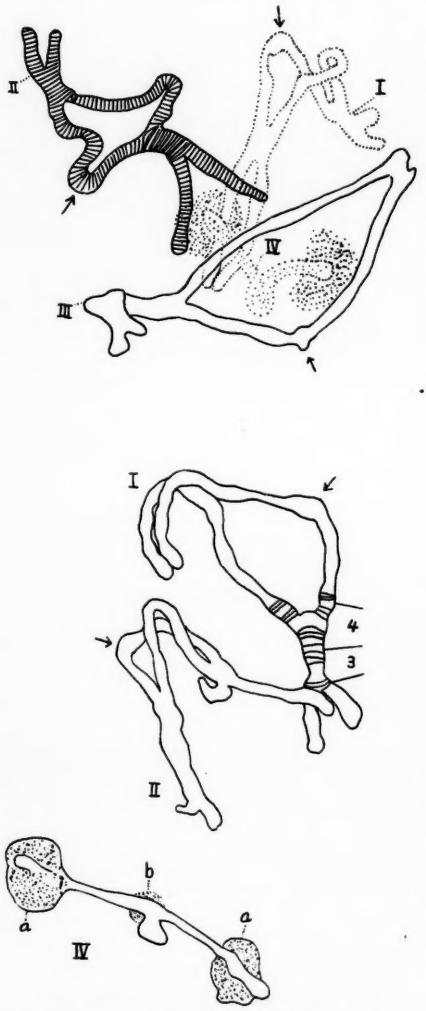


Figure 10 (*Legend on opposite page*)



OUTLINE DRAWINGS OF NUCLEI
Figure 11

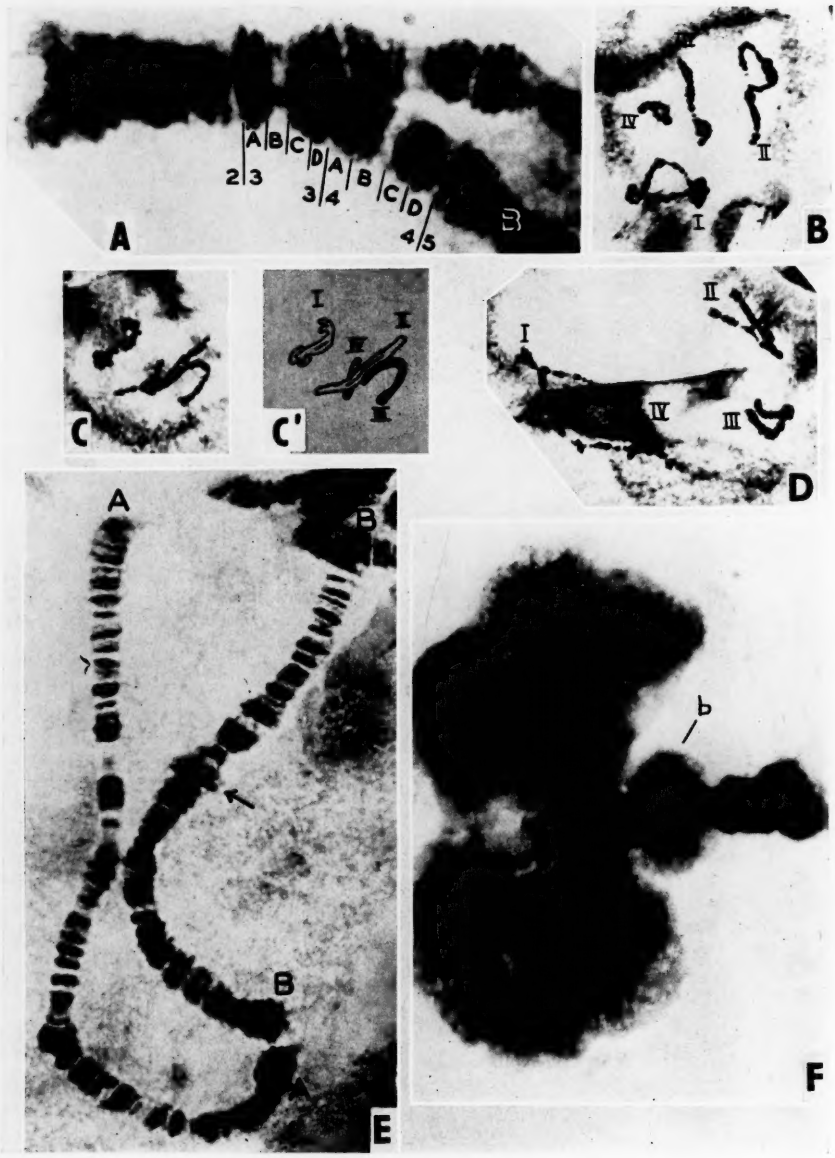
Outline drawings of Figure 10*B* and *D* on opposite page.

vestigated. As shown in the Figures 10-11, pairing is discontinuous in all four chromosomes. In the three long chromosomes there is as a rule one large unpaired region in the middle, while the ends are paired to a varying extent, loose association alternating with synapsis. Comparison of numerous nuclei revealed that pairing conditions vary not only from animal to animal but also in different nuclei of the same gland. Figure 15 is a diagrammatic representation of the pairing conditions in ten instances in each of chromosomes I, II, III. While the distribution of loose pairing and synapsis seems particularly variable there appears to be one constant feature: In a large central region of each long chromosome pairing is always absent. For chromosome III the map of this non-homologous section is presented in Figure 13*AB*. The numbering represents a provisional attempt at homologizing sections. The differences are probably too large to allow of more than a rough comparison. The lack of resemblance in this area is obvious in Figures 14 and 10*A* and particularly in Figure 10*E*, where the two non-homologous regions are accidentally closely approximated. One relatively constant feature is the configuration of region 4 in chromosome I where partners separate as a general rule, though no obvious difference has so far been detected in the banding. Figure 12*A* shows this area highly magnified. Figure 10*D* may be consulted for comparison. A still greater agreement is shown in section 27 of chromosome II.

It might be suggested that the wide range of variation in pairing is due to differences in the pressure exerted on the pairs during preparation of the

SYNAPSIS OF HYBRID CHROMOSOMES
Figure 10

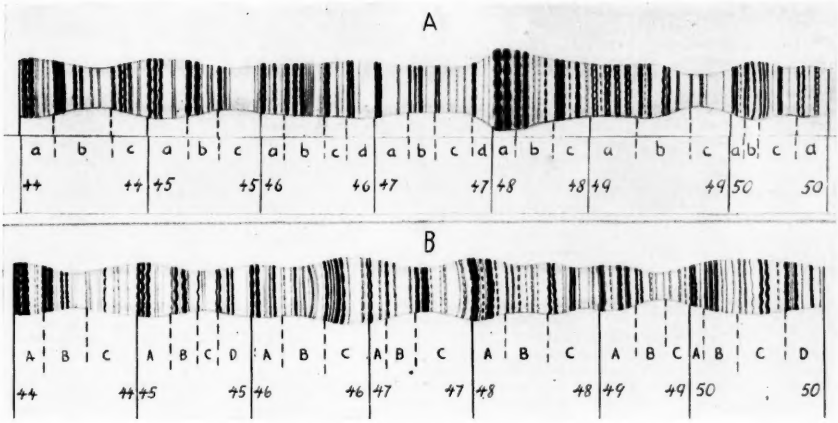
A—Hybrid Chromosome III, showing synapsis in three regions only. × 900. (Drawing of this chromosome is shown in Figure 14.) *B*—The nucleus of a hybrid gland. All four chromosomes are shown. The nucleolus is double. Throughout the figures the arrows indicate the central bumps of strain *B*. (An outline drawing of this nucleus is shown in Figure 11*A* above) × 500. *C*—The Malpighian nucleus of a hybrid. All four chromosomes show intermittent pairing as seen in salivary nucleus. × 680. *C'*—Shows a drawing of this nucleus. *D*—Chromosomes I, II, IV, of a hybrid gland. *a* shows the main nucleolus doubled and *b* shows an accessory nucleolus (Balbiani's ring) single. × 500. *E*—Shows the unpaired central region of hybrid chromosome III. The two partners are accidentally approximated. × 2,400.



HYBRID CHROMOSOMES

Figure 12

A—Detail of hybrid chromosome I. Note obvious difference in section 4 of the two partners. × 1,800. *B-D*—Three nuclei of a backcross individual. Note the correspondence in pairing conditions. Chromosomes I and II are hybrid; chromosomes III and IV synapsed. × 1,900. E—Hybrid chromosome III with a minimum of association between the partners. × 870. *F*—Hybrid chromosome IV, with one end synapsed and the other unpaired. Main nucleolar mass is partly divided. A small accessory nucleolus (Balbiani's ring) is shown at *b*. × 1,800.



BANDING OF CHROMOSOMES COMPARED

Figure 13

Maps of the central regions of Chromosome III of strains *A* and *B*. The banding at the left end is quite similar but marked differences in the pattern of the banding along the chromosome can be seen.

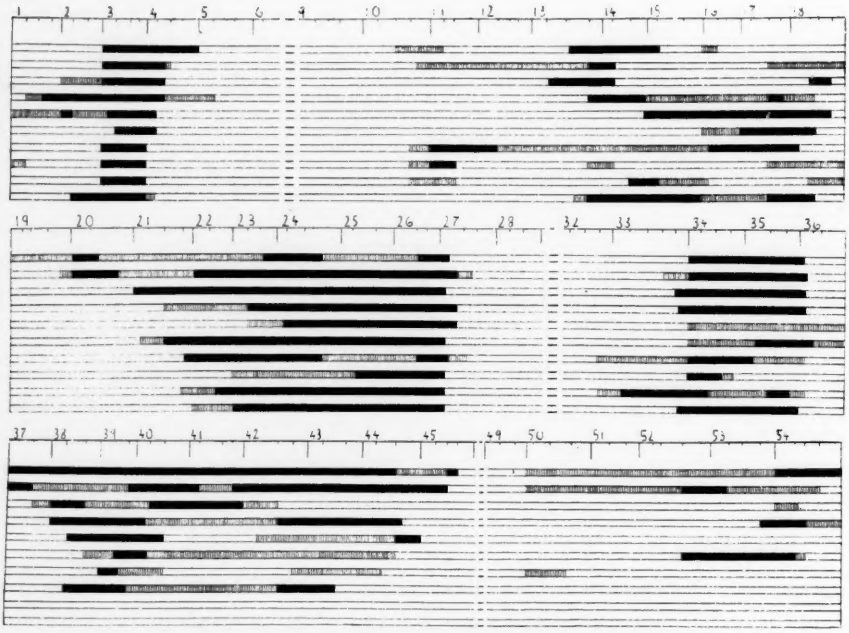
CAMERA LUCIDA DRAWING OF CHROMOSOME III

Figure 14

This shows the paired chromosomes in a hybrid between strains *A* and *B*. The photograph of this chromosome is shown in Figure 10*A*. Compare with map above.

smears. However, this factor can be only partly responsible for the differences observed. For in some preparations which otherwise show no signs of excessive pressure, synapsis is very limited in all nuclei of the gland, while in others though strongly pressed and stretched the union of the pairs has remained firm. An interesting condition is shown by a gland in which all nuclei have the partners of chromosome III almost entirely separate (Figure 12*E*). Obviously, the incongruity of the middle part has a tendency to interfere with the synapsis of the more homologous terminal regions. It could not be decided whether a "time-limit" of pairing as suggested by Darlington[7] comes into play in these hybrid glands.

One of the most outstanding differences in the banding pattern of all three pairs in both wild type and in the hybrid is the characteristic "bump" of the central region of strain *B* which is appar-



PAIRING CONDITIONS IN HYBRID CHROMOSOMES
Figure 15

The three segments of this map show the conditions in chromosome I (1-18); chromosome II (19-36); and chromosome III (37-54). White shows the unpaired regions; shaded shows the loosely associated regions; and black shows the synapsed regions in these chromosomes. In spite of the close similarity of these two strains, a very considerable difference is shown in the chromosome structure of all three of the larger chromosomes.

ently absent in strain *A* (Figures 10*B*, 10*D*, 10*E*, 12*E*). The bump is likewise present in the parental *A* strain and absent in the parental *B* strain. Bauer has suggested that these bumps might contain the spindle attachments, which have not been definitely located in *Chironomus thummi*. If this hypothesis is correct, the present races differ markedly in the structure of the spindle attachment region.

Chromosome IV in the hybrids deserves special attention. It is always unpaired at the end that is associated with the main nucleolus. This is the same region that may remain unpaired in homozygous IV chromosomes; but the heterozygous nature of the two unpaired limbs manifests itself in a tendency of the nucleolus in smears, to divide partly (Figure 12*F*) or completely (Figure 10*D*) into two distinct masses, each in contact with one chromosome partner. Thus, the normal aggregation of the nucleolar mass is interfered with by the incongruity of the chromosome regions with which it is associated. However, the small accessory nucleolus (Balbiani's ring) which is in connection with a synapsed chromosome region, appears single.

As a confirmation of the observations on F_1 hybrids, the nuclei of back cross individuals were examined. All expected Mendelian combinations of paired and unpaired chromosomes were found. Three nuclei from one individual with similar pairing conditions are shown in Figure 12*B-D*. This proves that it is not a "cytoplasmic factor" or an upset of balance in the genes concerned with synapsis that produces the characteristic

pattern of the hybrid. Transitions between the typically hybrid and the perfectly synapsed state were also observed. This is what ought to be expected on the assumption that crossing-over occurs freely in the hybrid males. For the purpose of the table given below, a chromosome was classed as "paired" when synapsed over 5/6 of its length. Though the number of individuals examined was small, the deviation from the expected Mendelian ratios again points to a high cross-over rate.

Giant nuclei built on the same plan as the salivary nuclei were found in various somatic tissues of different Diptera by Geitler,[10] Makino[15] and Berger.[5] In the present strains of Chironomus, giant cells occur in the fat body, cerebral ganglia, cardiac part of intestine, hindgut and Malpighian tubules. Those of the hindgut and Malpighian tubules are particularly large and four chromosomes can be identified in them. As would be expected in hindgut and Malpighian tubules of hybrids, pairing conditions are the same as in the salivary gland. (Figure 10*C*).

Discussion

Although inversions are reported to be frequent among Chironomids, no indications of either inversions or translocations have been found in the present hybrid. Thus it differs markedly from all known Drosophila hybrids; however, it seems to bear resemblances to the *Sciara* hybrid described by Metz and Lawrence.[16] Much examination of details remains to be done, but all appearances indicate that here as in *Sciara* the development of the two strains from a common ancestor was brought about by a multitude of minute rearrangements and perhaps of gene mutations. In *Drosophila* a similar mechanism seems to be at work side by side with that of large aberrations. Bauer observed that 13 out of 16 species of Chironominae investigated agreed in the general features of the caryotype. This would seem to exclude a high occurrence of large aberrations. However, by comparison of the salivary patterns, Bauer came to the conclusion that large transpositions did occur but tended to be intra-chromosomal. In view of the complicated systematics of such a highly successful and widespread genus as *Chironomus* further investigations of crossability seem desirable.

While the cytological results resemble those in *Sciara* the genetics differ. Of the *Sciara* hybrids, only the males are partly fertile and these are "genetically pure." In *Chironomus,* on the other hand, hybridity does not apparently interfere with reproduction. In view of the considerable divergence in chromosome structure and affinities, the high fertility of this hybrid appears noteworthy.

No explanation can be offered for the restriction of hybridity to the intercalary regions of the three long chromosomes. It is also difficult to estimate the effect of this condition on meiosis. On the one hand, the possibility of forming subterminal chiasmata seems favorable; on the other hand, prophase pairing ought to be seriously handicapped by the absence of synaptic affinity in this section, because in the majority of cases it starts in the spindle attachment region.[7] While meiosis in *Chironomus* has not yet been described, Koller[13] observed in the development of *Drosophila* salivary glands that synapsis begins in the centromere region.

Summary

1. Two strains of *Chironomus* were crossed and fertile hybrids were obtained.

2. Normal F_2 and F_3 individuals resulted from further crossing.

TABLE I. Chromosomes in back-cross individuals.

Number of chromosomes paired	0	1	2	3	4	Total
Individuals obtained	2	13	19	4	3	41
Percentage obtained	4.8%	31.7%	46.3%	9.8%	7.3%	100%
Percentage expected	6.3%	25%	37.5%	25%	6.3%	100%

3. In the three long chromosomes of the F_1 hybrid, synapsis is absent in certain central regions. In the terminal regions pairing is discontinuous and shows much variation in different nuclei.

4. The nucleolar mass appears partly or wholly divided, owing to the lack of homology in one end of chromosome IV.

5. Nuclei of backcross individuals show paired and unpaired chromosomes in roughly Mendelian ratios.

6. There are indications of crossing-over in the F_1 males.

7. Strong divergences in the salivary pattern of the two strains are revealed by comparison of the unpaired central regions.

8. Intermittent synapsis is also found in giant cells of the Malpighian tubules and of the hindgut of hybrids.

9. The apparent absence of large chromosome aberrations in this hybrid is discussed.

10. The effects of the homology of the terminal regions on chiasmata formation and consequently on hybrid fertility are considered.

Literature Cited

1. Bauer, H. Die Speicheldruesenchromosomen der Chironomiden. *Naturwiss.* 233, 1935.
2. ————. *Zeitscht. Zellforschung* 23. 1935.
3. Beitraege zur vergleichenden Morphologie der Speicheldruesenchromosomen. *Zool. Jahrbuch Phys.* 56. 1936.
4. ————. Cytologie. In *Fortschr. d. Zool.* I. 1937.
5. Berger, C. A. *Jour. Hered.* 31. 1940.
6. Bridges, C. B. *Jour. Hered.* 29. 1938.
7. Darlington, C. D. Recent advances in Cytology, 2nd edition. London.
8. Dobzhanski, Th. and D. Sokolov. *Jour. Hered.* 30. 1939.
9. Dubinin, Sokolov, Tiniakov. *Nature.* 1936.
10. Geitler, L. *Zool. Jahrbuch Phys.* 54. 1934.
11. ————. Chromosomenbau. Protoplasma Monographien 14 Berlin. 1938.
12. *King, R. L. and H. W. Beams. *Jour. Morph.* 56. 1934.
13. Keller, P. C. *Proc. Roy. Soc.* Series B. 810. 1935.
14. ————. *Jour. Genetics* 32. 1936.
15. Makino, S. *Cytologia.* 1938.
16. Metz, C. W. and E. G. Lawrence. *Jour. Heredity* 29. 1938.
17. Metz, C. W. Proc. 7th Internat. Genetical Congress. 1939.
18. Muller, H. J. In "The New Systematics." Oxford. 1939.
19. Paetau, K. Chromosomenmorphologie bei Drosophila melanogaster und Drosophila simulans. *Naturwiss.* 23. 1935.
20. Sadler, W. O. *Cornell University Memoirs* 173.
21. Sturtevant, A. H. and Th. Dobzhanski. *Proc. Nat. Acad. of Science.* 22. 1936.
22. Tan, C. C. *Proc. Nat. Acad. of Science* 21. 1935.

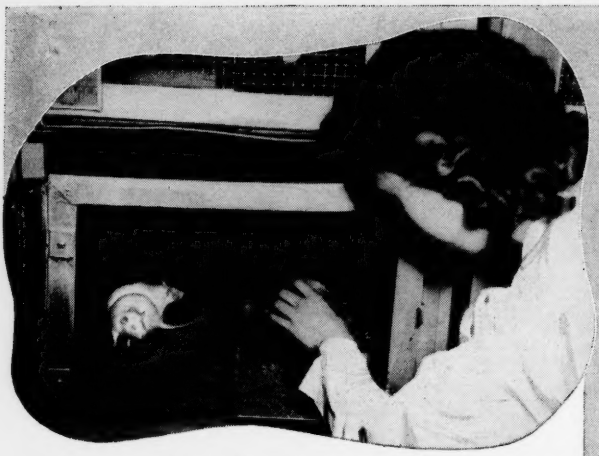
*The originals of these papers were not available to the author.

✦

Manx Genetic Injustice

The New York Times Book Review Section records a notorious instance of genetic maldistribution. It is incorporated in a ditty popular at the Training School of the British Marines, who devil-dog like, are out to set this wrong right:

Are you are that the cats have got no
Tails in the Isle of Man?
All the other cats have tails,
In England, Ireland, Scotland, Wales.
It seems a gross injustice.
To right it is our plan.
Are you are that the cats have got no
Tails in the Isle of Man?



NO MIXING
NO MEASURING
NO MUSS

Complete Feed For:

Rats, Mice, Monkeys, Dogs, Cats

Complete Feed For:

Guinea Pigs, Rabbits

Easy-to-Feed, Controlled Rations

Why bother with mixing, weighing, cooking, cleaning up? Save the time assigned to these operations, and provide a complete ration, as nearly controlled as is practicable. Write for free sample, costs, and feeding directions. Address Purina Mills, St. Louis, Mo.

PURINA LABORATORY CHOWS

INBRED MICE

FOR RESEARCH IN EXPERIMENTAL BIOLOGY AND MEDICINE

DURING the past few years this Laboratory has completed the establishment of a number of inbred and hence genetically homogeneous strains of mice which have proven extremely valuable for research in experimental medicine and biology. The inbreeding is carried on through repeated brother times sister matings. The essential consequence of the inbreeding is that the individuals within a strain become increasingly uniform in their heredity and after twenty generations may be regarded for all practical purposes as genetically identical. The use of such material largely eliminates a common source of difficulty in biological investigations, namely, the inherent variability of the organisms ordinarily available. The uniformity of inbred strains is illustrated by the fact that tumors originating in such a strain, when transplanted, will grow in 100% of the individuals of that strain, but will grow irregularly if at all in other strains.

Careful checks are maintained on the homogeneity of the strains carried by this Laboratory. Sublines tend to develop within an inbred strain due to the accumulation of minor mutations. These are detected and where advisable eliminated through the use of appropriate tests and breeding methods.

The Laboratory will welcome inquiries from scientific laboratories and hospitals concerning the inbred stock available or with regard to the possibility of providing stocks and types suitable for special experimental problems.

Supply Department

ROSCOE B. JACKSON MEMORIAL LABORATORY

Bar Harbor **Maine**

"HEREDITY" LANTERN SLIDES

MAN

16-397. Gregor Mendel's Handwriting — First Page of "Studies of Plant Hybrids".
17-435. Merton House—Home of William Bateson.
21-1-Cover. The "Fuchsia-Picture" of Mendel.
21-No. 2-Cover. Francis Galton.
26-158. Ishmael Family—Six Generations of a Degenerate Family.
26-159. Roosevelt Family—Pedigree Chart of a Superior Family.
26-292. Dr. and Mrs. Hugo de Vries.
15-330. Fused Finger Joints.
17-393. Short Legs—Inherited Achondroplasia.
20-75. Extra Fingers—Recessive Polydactylism.
20-74. Chart Showing Inheritance of Polydactylism.
20-352. A Folding Man — Hereditary Absence of Clavicles.
22-104. Crooked Arms and Legs—Hereditary Bone Fragility.
23-307. Five Generations of Glaucoma.
23-425. Inherited Doublejointedness in the Thumb.
24-269. Chart Illustrating Sex-Determination.
22-47. Palm Prints of Fraternal Twins.
22-40. Corresponding Fingerprints of 3 Pairs of Identical Twins.
23-369. Identical Twins—Separated 13 Years.
23-2. Identical Twins Reared Apart—Mary and Mabel when Grown.
23-5. Identical Twins Reared Apart—Mary and Mabel as Babies.
23-6. Identical Twins (Mary and Mabel) at Two Years—Reared Apart.
23-8. Palm Prints of an Identical Twin (Mary).
23-9. Palm Prints of an Identical Twin (Mabel)
24-443. Mirror-Imaging in Eye Dominance in Identical Twins.
24-444. Table Classifying Handedness in Twins.
25-140. Table of Physical Characteristics of Identical Twins Reared Apart.
25-141. Identical Twins (Harold and Holden) Reared Apart.
25-293. Retina of Normal and Albino Eyes.
25-332. Abnormal Fingers and Toes — Syndactyly, Camptodactyly, and "Hammer Toe".
25-333. Short Finger (Brachymetapody) due to short metacarpal bone.
25-391. Hereditary Absence of Incisors.
25-446. Inherited Chest Depression—Koilosternia.
25-483. Sex-Linked Toothlessness.
25-338. Fifty-fifty Segregation for Woolly Hair Mutation.
26-143. Extra Toes—Inherited Polydactylism.
10-389. Twin Acrobats—Identical Twins.
10-409. Typical Identical Twins.
20-50. Identical Twins Reared Apart.
20-52. Palm Patterns of Identical Twins.
20-155. City Boy and Country Boy—Identical Twins Reared Apart.
20-160. Enlarged Prints of Left Ring Finger of Identical Twins (C & O).
22-202. The Hilton Siamese Twins.

ANIMAL

16-154. Pelvic Bones of Normal and Rumpless Fowls.
16-352. Leg Bones of "Reptilian Fowl" and of Normal.
19-413. A Fertile Mare Mule.
19-414. "Old Beck" (Mule) and Her Horse-Like Colt.
19-415. Mule-Like Colt of Fertile Mare Mule.
20-112. Recessive Leg Feathering in Fowl.
20-113. "Heel Tufts" in Fowl.
21-323. Heterogeneous Chromosome Structure — Irregular Cell Division in Drosophila Melanogaster.
22-213. Conjoined Twins in Cattle.
22-296. Backcrosses between Hybrid (Zebu × Yak) Female × Zebu Male.
22-298. Zebu Bull Used in Yak Crosses.
22-299. Yak Cow Used in Zebu Crosses.
22-305. A Zebu-Yak Hybrid—4 Years Old.
22-305. Zebu-Yak Hybrid Cow—4 Years Old.
23-449. A "Flightless" Rooster.
24-183. Parallel Color Mutations (Himalayan and Siamese) in Rabbit and Cat.
25-208. Five Generations of Inbreeding—Shorthorn Cattle (chart).
25-266. X-Ray Photos of Normal and "Flightless" Feathers in Fowl.
25-435. Production of Agglutinins in Rabbits (chart).
25-432. Agglutination of Incompatible Bloods.
25-464. "Portraits" of Salivary Gland Chromosome.
25-466. Giant Chromosomes Compared with "Normal".
25-469. Synapsis of Normal and Inverted Chromosomes.
25-470. Synapsis of Deleted and Normal Chromosomes.
25-472. Cyto-Genetic Maps of Salivary Chromosomes. (Insert.)
26-62. Salivary Chromosomes and Gonial Chromosomes Compared.
26-62. Reference Map of the Salivary Chromosomes of Drosophila. (Insert.)
26-182. Structure of Salivary Gland Chromosome.
26-301. Effects of Sex Hormone Injection on Feather Growth.

PLANT

15-204. Capsules of Globe Daturas.
17-372. Awn of Manchuria (Rough) Barley.
17-373. Awn of Lion (Smooth) Barley.
18-128. Adaptive Cupped Tendrils of a Plant.
18-129. Adaptive "Vacuum Cup" Toes of a Toad.
18-382. Leaves of Live Oak × Post Oak Hybrids.
18-383. Leaves of Overcup × Live Oak Hybrids.
19-419. "Fatback" and "Razorback" Honey Locust Pods.
20-24. Haploid and Dwarf Diploid Tomato Plants.
20-25. Haploid and Normal Tomato Plants.
20-26. Haploid and Diploid Tomatoes.
20-206. Flax Hybrid Produced by Artificial Nutrition.
22-368, 370. Plant Patents No. 2 and No. 3.
24-131. Radium-Induced "Ridged" Tomato.
24-133. Chimeral Radium-Treated Tomato Leaves.
24-134. Radium-Induced Virescent-White Tomato Seedlings.
24-368. Gene Mutation Chimera in Delphinium.
26-137. Ears of Maize, Relatives, and Hybrids.
25-448. Fasciated Sugar Beet.

Above are listed ninety Lantern Slides from JOURNAL OF HEREDITY illustrations. These are only a sample of over five thousand charts and photographs which have been published in the twenty-six volumes of the JOURNAL. Order from this list by Number. Slides may be ordered for any illustration appearing in the JOURNAL by giving Volume—Page—and Figure Number. Slides on this list will be supplied within a week of receipt of order. Price 75c each —$8.00 per dozen. Slides are numbered according to volume and page on which they appear. Thus 25-372 is from Volume 25, page 372 of the JOURNAL, 24-300 is from Volume 24, page 300, etc. Suggestions for illustrative material from the JOURNAL suitable for specific lectures will gladly be furnished on request. Address orders and send for list of 250 slides to:

AMERICAN GENETIC ASSOCIATION

1108 Sixteenth St., N. W. **Washington, D. C.**